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Mountain Pine Beetle Dynamics in Lodgepole Pine Forests Part III: Sampling and Modeling of Mountain Pine Beetle Populations

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RESEARCH SUMMARY

Much of this work is original research by the authors. However, published literature on sampling and modeling of mountain pine beetle populations is reviewed primarily for epidemic beetle populations in lodgepole pine forests. Sampling methods are available for within-tree populations of beetles, for ground surveys of tree losses in stands, and for aerial surveys to estimate tree losses over large areas. Models are presented for beetle survival, beetle dispersion, beetle aggregation, lodgepole pine stand-beetle interactions, and rate of tree loss to improve existing risk-rating models.

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COVER PHOTO: Lodgepole pine trees killed by mountain pine beetles on the Targhee National Forest in southeastern Idaho. INSERT: Lodgepole pine felled and sampled for mountain pine beetles.

PREFACE

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a native bark beetle whose depredations cause various effects upon the lodgepole pine, *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm., ecosystem. Historically, the beetle kills millions of trees each year in the United States and Canada. During epidemics, a single National Forest may lose in excess of a million trees in a single year; for example, 3.6 million lodgepole pines were killed on the Targhee National Forest, ID, in 1976 (Klein and others 1978). The mountain pine beetle has killed an estimated average of 2 billion bd ft per year since 1895 (Wood 1963). In 1970, volume loss of growing stock to all mortality causes totaled some 613 million ft^3 (17.4 million m^3) within the Rocky Mountain States; this is equivalent to nearly 75 percent of the volume of roundwood produced. In the same year, sawtimber volume losses were 208 million ft^3 (5.9 million m^3), equivalent to nearly 50 percent of the volume of roundwood products from sawtimber (Green and Setzer 1974). The mountain pine beetle in lodgepole and ponderosa pines accounted for about 473.3 million ft^3 (13.4 million m^3) or 77 percent of this volume loss. Similar losses could be expected in the West Coast States. In western Canada, losses of lodgepole pine to the mountain pine beetle were estimated to be 1.3 million ft^3 (36 900 m^3) per year between 1950 and 1970 (Safranyik and others 1974). This impact places the mountain pine beetle as the prime insect agent affecting the lodgepole pine ecosystem. The effects of beetle infestations change the entire lodgepole pine environment and, depending on subsequent occurrence or exclusion of fire, largely determine the nature of successional dynamics—enhancing lodgepole pine renewal in the case of fire, or succession of more shade-tolerant species in the absence of fire.

Tree mortality in pine stands can occur as scattered individual trees, but more often trees are killed in groups. Unchecked, these groups expand with succeeding beetle generations, and eventually large areas may suffer extreme losses of their forest cover. This may or may not be catastrophic, depending on landowner objectives. Some landowners, for example, favor grassland over timberland and a bark beetle outbreak may be beneficial to them. On the other hand, the value of a mountain home may be severely reduced by the death of high-value shade trees, and the owner may view this loss as highly undesirable. From the timber-producer standpoint, the beetle can disrupt management plans and cause an unwelcomed impact on local, regional, and national economies.

This treatise represents much original research by the authors, but it also is a review of other published literature about the mountain pine beetle, with particular reference to epidemic infestations. Much research remains to be done in testing and applying management strategies indicated by this research. In addition, the dynamics of mountain pine beetle populations during endemic periods are in need of study. During periods of low beetle activity, we believe significant "keys" exist that will permit more effective management of stands to prevent increases in beetle populations.

Our research approach first addressed the recognition and determination of relationships between the insect and its associated environmental factors. These relationships, based on biological functions, were studied to determine their biological effect upon the insect. Second, quantification of these relationships was based upon measurement units relative to beetle behavior. The host variable was considered as an integral unit within the ecosystem.

Our intent is to lead readers through this maze of interactive relationships to the extent of their interest and existing knowledge. With this in mind, we have prepared three publications, the last of which is this current one:

Part I. Course of Infestation—including beetle impact on the lodgepole pine stand, how the beetle "moves through" the stand, expected timber mortality, and management alternatives.

Part II. Mountain Pine Beetle Population Dynamics—including bionomics, analyses of mortality factors, entomological relationships, and the "inner workings" of a mountain pine beetle population.

Part III. Sampling and Modeling of Mountain Pine Beetle Populations—including methods of sampling and modeling both lodgepole pine and mountain pine beetle populations.

Mountain Pine Beetle Dynamics in Lodgepole Pine Forests Part III: Sampling and Modeling of Mountain Pine Beetle Populations

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SAMPLING

Sampling—the foundation of any mensurational aspect of population ecology—is basic to subsequent steps in evaluating actions and interactions of individual factors, groups of factors affecting population behavior, and subsequent model building. Sampling schemes and sample units should be based on the behavior of the insect and used as mensurational and analytical tools to provide accurate and realistic insight into populations of insects. Such "behavioral sampling units" must have biological relativity to the insect-environment association and, in particular, to the life processes of the insect (Cole 1967).

The use of area samples alone may have little biological meaning in reference to a particular insect. The number of bark beetles per unit area merely indicates the density of the insect population, which, although desirable in many cases, may only reflect convenience to the sampler. Expressing a population with respect to an area (that is, as absolute density) neither describes the differing biological implications of individuals living in an association nor the insect-host biological relationship. Therefore, the principal objective of any sampling procedure is to secure a sample that, subject to physical limitation, will reproduce the characteristics of that population as closely as possible.

Our approach to studying the dynamics of mountain pine beetle populations involved two main sampling procedures: (1) the sampling of stands to determine the characteristics of trees and stands infested by mountain pine beetles, and (2) the sampling of beetle populations within trees to determine factors affecting natality and mortality and for predicting population trends.

A distinction is made here between sampling for population dynamics research purposes and sampling for trend prediction in surveys. The requirements for the two are substantially different. The first attempts to define the real causes of population fluctuations; the latter is more directly involved in applied forest entomology. However, once the causes of population fluctuations are determined, then reliable sampling schemes for trend predictions can be readily developed.

Sampling Stands

Sampling stands can be done by ground surveys where limited area is involved and detailed measurements of trees are needed, or by aerial surveys where large areas are involved and less detailed tree information is required.

Ground surveys.—Most sampling of mountain pine beetle-infested trees has been directed toward estimating the incidence of attacked trees. The primary use of results was for planning control operations. Survey methods were usually the "line-strip" or "strip-plot" methods. Knight (1958) compared three plot sizes and two strip widths for estimating mountain pine beetle-infested trees in ponderosa pine stands. These were:

—0.1-acre (0.04-ha) plots at 2-chain (40-m) intervals along parallel cruise lines.

—0.2-acre (0.08-ha) plots at 2.5-chain (50-m) intervals along parallel cruise lines.

—0.25-acre (0.10-ha) plots at 2.5-chain (50-m) intervals along parallel cruise lines.

—Parallel cruise lines of 0.5-chain (10-m) width.

—Parallel cruise lines of 1-chain (20-m) width.

Knight (1958) concluded that the five methods gave approximately equal results when the same number of cruise lines were used. He stated that although no method was superior, results favor the 0.5-chain strip method. It and the 0.1-acre plot method will be conducted faster than the other methods, but the 0.5-chain strip method was selected because inexperienced personnel could be trained more quickly to obtain accurate results. Sampling errors for all methods were influenced by acreage, survey coverage, and number of trees infested.

Parker (1972) tested the 0.1-acre fixed plot, 0.5-acre (0.20-ha) strip plot, and two variable plot sizes of 5 basal area factor (BAF) and 10 BAF to determine which gave the best estimate of lodgepole pine losses to mountain pine beetles. These were compared to a tally of all infested trees within the study area. Parker found no appreciable differences among these methods in estimating numbers of trees killed per acre by mountain pine beetles. Losses estimated from the 0.5-acre strip plot method correlated closer with the tally of all infested trees, but more time was required for plot measurements.

Initially, we (Cole and Amman 1969) settled on line-plot sampling using 0.1-acre fixed radius plots. Plots were located equidistant on parallel lines throughout the area of interest. The 0.1-acre plots were thus in a grid pattern. The fixed radius plots were selected because more small diameter, infested trees would be measured than with variable plot cruising. We were especially interested in the small diameter trees because mountain

pine beetle epidemics rarely, if ever, start in stands consisting of small diameter trees. We were interested in knowing:

1. Types of trees the mountain pine beetle kills.
2. Beetle production in different types of trees.
3. Tree characteristics associated with high brood production.

Initially, 20 plots of 0.1 acre (0.04 ha) fixed-diameter were systematically located in a grid pattern within a 2-mile (3.2-km) square unit (Cole and Amman 1969). We initially chose the large area because we wanted to sample beetle losses over the full range of stand conditions one might encounter in lodgepole pine stands. From this information we could explore tree losses in relation to elevation, stand density, and stand structure. Beetle production could be measured on each infested tree and related to the above factors, as well as to individual tree characteristics.

All trees within the sample plot were recorded by (1) diameter at breast height, (2) total height, (3) crown class, (4) living or dead, (5) year of death, and (6) cause of death. Year of death, if there was a need to postdate death, was estimated by foliage, twig, and other characteristics: (1) foliage green, fresh boring frass, larvae or eggs present—killed in current year; (2) foliage bright orange to straw color—killed in previous year; (3) foliage dull orange and most retained—killed in second year past; (4) foliage dull orange to gray and most lost—killed in third year past; (5) no foliage, most small twigs supporting needle fascicles lost—killed in fourth year past; (6) many larger twigs lost, bark peeling—killed in fifth year past or before. Parker (1973) said he could not accurately determine year of death for trees that died more than 1 year previously. However, the close resemblance of curves showing loss by year of death by Cole and Amman (1969) and information in Gibson (1943) suggest that the criteria used by Cole and Amman for dating year of tree death are reasonably accurate.

Estimates of the average diameter of trees killed by the beetle per year gave coefficients of variation that were usually less than 10 percent.

As scientists have gained knowledge about the mountain pine beetle, estimates have been improved by stratifying according to various factors that influenced tree losses—for example, elevation (Amman and Baker 1972) and habitat type (Roe and Amman 1970; McGregor 1978; Cole and McGregor 1983). The procedure for estimating lodgepole pine losses to mountain pine beetles in Forest Service Northern Region is to use ten 10-BAF plots located in a grid pattern within a habitat type (McGregor, personal communication, April 1982). However, once again, a reminder that the aims of survey and research purposes are different and, consequently, may dictate different sampling schemes.

Aerial surveys.—Ground surveys for estimating tree mortality and trends in mountain pine beetle infestations proved quite acceptable for small areas or single stands. However, the areas sampled usually represent a small portion of the total acreage infested during a beetle outbreak. For large areas, large-scale color aerial photography using 70 mm or larger format has proved quite efficient for detecting beetle-infested or killed timber (Wear and others 1966).

Color and black and white films were tested at two scales (1:7,920 and 1:15,840) to detect ponderosa pine killed by mountain pine beetle in the Black Hills (Heller and others 1959). There was no significant difference among estimates by observer, but a highly significant difference between films. Panchromatic film gave poor results, whereas Ektachrome yielded excellent results. Using color film, experienced interpreters obtained estimates within a 5 percent error.

Estimating dead trees more than 1 year old from true color aerial photos at scales of 1:1,600 and 1:2,400 presents some serious problems. For example, a high percentage of trees are missed and others are incorrectly identified (Hamilton 1981).

A color stereophotographic procedure using a 35-mm camera from light aircraft to quantify mountain pine beetle-killed lodgepole pine was developed (Klein 1973). Mortality estimates from photos were highly correlated with ground counts ($r^2 = 0.90$), and the highest correlation was new faders ($r^2 = 0.94$). Photo counts usually were less than ground counts, but these errors of omission were attributed to small dead trees in the understory that were not visible to the camera. The effectiveness of aerial measurement technique, applied in the framework of double sampling designs, can aid tremendously in estimating total tree loss within large management units. This method was further refined with high altitude, panoramic photography using KA-80A optical bar photography as an alternative to frame photography. The panoramic color IR aerial photography provided the data base for a multistage survey using probability proportional to size (PPS) at three levels to estimate numbers of trees and volume killed. Standard errors using this method were 10.3 percent for number of trees killed and 13.6 percent for volume estimates. These errors were judged quite acceptable (Klein 1982). The greatest handicap of aerial methods is that trees infested the year before are counted; thus, data obtained are almost 1 year old. Consequently, time is limited to make and implement management decisions before beetles emerge to infest green trees.

Sampling Beetle Populations

Sampling mountain pine beetle populations is accomplished primarily using the destructive sampling method of bark removal without replacement, but may also be done by indirect methods such as radiography. Sampling yields insights into causes of beetle mortality and trend in population change.

Bark removal method.—Sampling mountain pine beetle populations involves counting the beetles during various stages of the beetle's life cycle in sampling units within infested trees. Carlson and Cole (1965) developed a system for sampling mountain pine beetle in lodgepole pine trees. The experimental work was done within two stands, one on the Wasatch-Cache National Forest in northern Utah and the other on the Bridger-Teton National Forest in Wyoming. The insect populations were considered epidemic at that time.

The experiment was designed to test for variation between sample sizes, shapes, location within the tree, and diameter at breast height (d.b.h.) of the tree. Three variables were measured: (1) density of attacking parent beetles, (2) density of egg gallery, and (3) density of beetle brood. Six sample units were superimposed in nested fashion at each sample locus. Four of these were rectangular—0.1 ft^2 (93 cm^2); 0.25 ft^2 (232 cm^2); 0.5 ft^2 (465 cm^2); and a sample proportional to tree diameter. The other two sample units were circular—0.1 ft^2 (93 cm^2) and 0.25 ft^2 (232 cm^2). Each tree was sampled on the north and south aspects at breast height (4.5 ft or 1.4 m), 5 ft (1.5 m) below the top of the infestation, and midway between these points. Ten trees in each of the following d.b.h. classes were sampled in each study plot: 6 to 8.9, 9 to 11.9, 12 to 14.9, and greater than 15 inches (15.2 to 22.6; 22.9 to 30.2; 30.5 to 37.9; and greater than 38.1 cm).

Analysis of variance showed statistically significant differences among sample sizes, tree diameters, and study plots for attack and egg gallery densities, but showed no significant differences among sample sizes for brood density. Also, no differences occurred among sample heights for attack density; and only the middle and top sample heights differed significantly for brood density (tables 1, 2, 3).

The variances of attack, egg gallery, and brood densities were generally greater at breast height and mid-height than at the top. Overall, variance tended to be greatest at breast height, but since the mean values also tended to be larger at breast height, the coefficients of variation were not correspondingly high.

The larger the sample size, the fewer zero counts were recorded. Hence, the variance was more likely to be reduced. However, considering that the reduction in variance was rather minimal as sample size increased for attack, gallery, and brood densities, 0.25 ft^2 (232 cm^2) appears to be an acceptable sample size.

There was never complete consistency among aspects on the trees by plots. Therefore, random placement of samples by aspect was used.

The number of samples (trees) needed for a 20 percent standard mean error (SME) at the two-thirds probability level was computed for each sample size and all three variables at d.b.h. The north and south samples were combined because they were not random with respect to each other and in effect constituted a single sample. More samples are required for measuring attack density and gallery lengths for the smaller size sample than for the larger size. For measurements of brood density, the required number of samples decreased as sample size increased. Combining north and south samples at d.b.h. generally effected an increase in number of trees needed (table 4).

Sampling can be limited to the breast height region within infested trees and satisfy the requirements of efficiency and reliability in reproducing the characteristics of the population (Carlson and Cole 1965). In adhering to the principle of systematic random sampling, the sampling universe is defined as that subpopulation within a zone 1 ft (30.5 cm) above and 1 ft below breast height of infested trees. This zone was divided into four quadrants: north, east, south, and west. Using the 0.25-ft^2 (232-cm^2) sample, the zone was divided into four levels of 6 inches (15.2 cm) each, producing 16 sample loci. At each sampling date, two loci were selected at random for sampling without replacement. This plan for computing within-tree and among-tree variances allows for the determination of statistical distribution of the data.

Knight (1959) compared samples of mountain pine beetle progeny from different heights in ponderosa pine. He found that progeny numbers were fairly uniform

Table 1.—Analysis of variance for attack density per 1 ft^2 (930 cm^2) of bark

Source	Sum of squares	Degrees of freedom	Mean square	F
Plots	10,668.95	1	10,668.95	26.56**
Tree sizes	12,887.36	3	4,295.79	10.70**
Sample sizes	107,007.54	5	21,401.51	53.29**
PT	1,776.20	3	592.07	1.47
PS	2,491.72	5	498.34	1.24
TS	7,241.00	15	482.73	1.20
Error, PTS	6,020.75	15	401.38	
Subtotal	148,093.52	47		
Aspects	0.49	1	0.49	0.00
Levels	2,264.04	2	1,132.02	3.26*
AL	411.86	2	205.93	.59
AP	1,530.43	1	1,530.43	4.41*
AT	2,087.41	3	695.80	2.00
AS	1,066.13	5	213.23	.61
LP	3,727.52	2	1,863.76	5.37*
LT	2,949.48	6	491.58	1.42
LS	2,327.64	10	232.76	.67
Error, PTSAL	72,296.93	208	347.58	
Total	236,755.45	287		

*Significant at 0.05 level of probability.
**Significant at 0.01 level of probability.

Table 2.—Analysis of variance for mountain pine beetle egg gallery density per $^1/_{10}$ ft^2 (93 cm^2) of bark

Source	Sum of squares	Degrees of freedom	Mean square	F
Plots	180.85	1	180.85	4.86*
Tree sizes	8,774.88	3	2,924.96	78.68**
Sample sizes	5,751.00	5	1,150.20	30.94**
PT	4,140.86	3	1,380.29	37.13**
PS	84.08	5	16.82	.45
TS	423.13	15	28.21	.76
Error, PTS	556.89	15	37.13	
Subtotal	19,911.69	47		
Aspects	1.41	1	1.41	0.00
Levels	1,800.34	2	900.17	1.71
AL	243.13	2	121.57	.23
AP	2,786.93	1	2,786.93	5.30*
AT	194.61	3	64.87	.12
AS	40.54	5	8.11	.02
LP	119.15	2	59.58	.11
LT	4,236.78	6	706.13	1.34
LS	668.63	10	66.86	.13
Error, PTSAL	109,753.61	208	527.66	
Total	139,756.82	287		

*Significant at 0.05 level of probability.
**Significant at 0.01 level of probability.

Table 3.—Analysis of variance for mountain pine beetle brood density per 1 ft^2 (930 cm^2) of bark

Source	Sum of squares	Degrees of freedom	Mean square	F
Plots (blocks)	370,909,825.92	1		
Sample sizes	12,845,676.64	3	4,281,892.21	1.16
Error, PS	11,038,342.64	3	3,679,447.55	
Subtotal	394,793,845.20	7		
Aspects	17,908,167.36	1	17,908,167.36	5.32*
Levels	35,517,526.09	2	17,758,763.04	5.27*
AP	44,466,345.09	1	44,466,345.03	13.20**
AS	1,774,537.12	3	591,512.37	.18
AL	33,448,518.07	2	16,724,259.04	4.96*
LP	19,075,248.37	2	9,537,624.51	2.83
LS	1,364,835.05	6	227,472.51	.07
Error, PSAL	77,471,934.61	23	363,344.98	
Total	625,820,956.90	47		

*Significant at 0.05 level of probability.
**Significant at 0.01 level of probability.

Table 4.—The number of mountain pine beetle-attacked trees required to be sampled for a 20 percent standard mean error at two-thirds probability level based upon summed north and south samples at breast height (rectangular samples only)

		Sample size			
Density	Plot	$^1/_{10}$ ft^2 (93 cm^2)	$^1/_4$ ft^2 (232 cm^2)	$^1/_2$ ft^2 (465 cm^2)	Proportional to d.b.h.
Attack	Teton	9.13	3.36	2.42	3.13
	Wasatch	7.76	4.22	3.63	3.08
Gallery	Teton	6.40	5.71	5.56	4.67
	Wasatch	2.46	2.63	2.20	2.12
Brood	Teton	8.19	9.93	8.16	7.56
	Wasatch	54.06	66.94	67.84	55.36

Note: Number of trees to be sampled should be rounded to nearest whole number for application.

throughout the infested portion of the tree trunk until April. By July survival was somewhat higher in the lower bole. He concluded that counting beetles in 50 samples, two 6- by 6-inch (232-cm^2) samples from each of 25 trees, gave reliable estimates of beetle numbers per square foot. The samples could be taken from the lower bole, 4 to 7 ft (1.2 to 2.1 m) above ground because population fluctuations at that point were similar to those in the upper bole. Populations of beetles in the infested trees in the fall and April were unrelated to infestation trend. However, populations on the same trees in July before the beetles emerged were directly related to infestation trend.

Sequential sampling.—Sequential sampling involves a flexible sample size instead of the fixed size required by conventional sampling. A number of units are examined until the cumulative number of beetles allows the infestation to be classified as increasing, decreasing, or static. Knight (1960) developed a sequential sampling plan for mountain pine beetle in ponderosa pine. Sequential sampling is not a research tool, but rather was developed for making biological evaluations. In order for infestation class limits to be developed, sampling of many infestations over several years is required so that population numbers can be related to changes in infestation status (Knight 1967).

The least work is required where population levels are extremely low or extremely high. Sequential sampling usually saves considerable effort by preventing oversampling. However, in infestations where a static condition is indicated, sampling may exceed that for a fixed size conventional method. Knight's (1960) sample was based on 0.25-ft^2 (232-cm^2) samples, two from each infested tree. An upper limit of 80 samples was specified so that if an infestation had not been classified by the time 80 samples were taken, the infestation was classified into the higher category. An error of classifying an infestation too high was considered more acceptable than classifying one too low.

Individual egg gallery sampling.—Biologically, it is of interest to know not only the densities of insects for a unit of space, but also the basic insect unit (individual, family, cluster) of a population. A technique to find such information is based on sampling individual egg galleries, each of which can be considered a "single family."

The pattern of egg deposition within a gallery and the distance between galleries set the stage for competitive interactions of larvae within and between egg galleries. In the past, we have based the intensity of competition upon the number of attacks per square foot (930 cm^2). However, sampling of individual egg galleries and their proximity to other egg galleries may give a better measure of competitive interactions (Cole 1967). The single gallery unit of measurement assumes that the effect of an ecological event on a "family unit" is representative of what would happen in an entire population that experienced a similar event.

Two generations (1965 and 1966) of the mountain pine beetle were sampled on three areas: Caribou, Teton, and Wasatch National Forests. Each generation was sampled three times—fall, spring, and summer—and, therefore, included counts of prewinter eggs and immature larvae, postwinter mature larvae, and mature larvae and pupae, respectively. The attack density and gallery length were also measured. Two sample units were taken from each of four trees, within each of three diameter classes—9, 12, and 15 inches (23, 30.5, and 38 cm) d.b.h. (table 5). Results obtained from sampling individual egg galleries were compared to those obtained from 0.25-ft^2 (232-cm^2) area samples (Cole 1970). Data from the 0.25-ft^2 samples were recorded in three ways: (1) average brood per 0.25 ft^2; (2) average brood per attack; and (3) average brood per inch (2.54 cm) of egg gallery.

Percentage of larval survival (table 6) was rather consistent in all measurement units, regardless of when the data were taken during the beetles' development. The less consistency and generally higher survival within the 15-inch (38-cm) diameter class are probably attributable to the increased attack density and the greater food quantity (phloem thickness) than found in 9- and 12-inch (23-cm and 30.5-cm) trees.

The encouraging aspect of these survival rates is their general similarity. Thus, one could use a single unit, or combined measurement units, to estimate survival, particularly for life table studies, and be reasonably assured of maintaining congruity between life stages. The information desired by the sampler, and time of year, will determine the selection of a measurement unit.

The single gallery sample provided the most representative data of the entire population but required additional biological measurement of attack density. Brood data from the 6- by 6-inch (232-cm^2) sample taken on an attack density basis provided the most statistically reliable information and encompassed the pertinent biological information. Percent survival, as could be used in elementary life tables, was rather consistent in all measurement units, regardless of when sampling occurred in the beetle's life cycle.

Radiographic sampling.—Following a cohort of bark beetles through development would be more desirable than obtaining sample estimates from different cohorts. Radiography makes possible such study of cryptic forest insects and has proved valuable in studying laboratory populations of bark beetles (Johnson and Molatore 1961; Berryman and Stark 1962). In addition, radiography has been used in the study of field populations by taking bark samples containing western or southern pine beetles into the lab for radiographing (DeMars 1963; Fatzinger and Dixon 1965). X-radiography was tried in seeking more accurate methods of sampling mountain pine beetle brood and their mortality factors.

In laboratory studies, results from radiographs of mountain pine beetle in infested bark and wood slabs varying in thickness from 1.5 to 2 inches (3.8 to 5.1 cm) showed that:

1. X-ray exposure adjusted for small differences in thickness and moisture content of wood and bark could yield readable radiographs.
2. An x-ray setting of 25 kilovolts (KV) was best when using the radiographs for counts of small- and medium-sized larvae. Either 25 or 45 KV could be used when radiographs were used to obtain counts of large larvae, pupae, and teneral adults.

Table 5.—Estimated means and standard deviations of mountain pine beetle brood units by diameter class, by season, and by measurement unit (years pooled)

Diameter class	Observation	Measurement unit[1]	Sample size	Estimated standard deviations: Among units within trees	Among units	Among unit totals	Mean
Inches			*(n)*	*(Sw)*	*(Su)*	*(Sy)*	*(y)*
9 (23 cm)	Fall	Single gallery	36	20.5	9.8	2.5	19.0
		B[2]	46	27.1	20.6	5.9	55.4
		BA	46	15.4	5.5	4.4	20.2
		BI	46	2.5	1.3	.2	2.8
	Spring	Single gallery	48	13.7	4.1	2.1	9.4
		B	46	18.9	17.9	4.7	19.0
		BA	46	11.1	7.2	2.2	6.1
		BI	46	1.2	.6	.1	1.0
	Summer	Single gallery	48	8.9	3.7	1.0	3.5
		B	48	11.7	4.4	1.4	11.0
		BA	48	4.5	1.7	.5	3.3
		BI	48	1.0	.6	.1	.6
12 (30.5 cm)	Fall	Single gallery	36	16.6	9.5	1.6	21.9
		B	40	64.1	39.5	4.9	67.8
		BA	40	15.9	8.5	3.2	21.6
		BI	44	2.4	1.3	.2	2.9
	Spring	Single gallery	40	7.1	1.8	1.0	7.3
		B	40	14.9	5.8	2.7	17.3
		BA	40	7.6	4.2	.8	5.0
		BI	40	.9	.5	.1	.7
	Summer	Single gallery	40	8.6	3.5	1.1	2.5
		B	40	8.9	3.3	1.2	12.4
		BA	40	3.4	.8	.6	3.7
		BI	40	.8	.4	.1	.4
15 (38 cm)	Fall	Single gallery	36	13.8	5.3	1.9	9.5
		B	36	41.3	12.3	5.2	35.1
		BA	36	13.5	7.1	1.4	8.3
		BI	38	1.7	1.0	.1	.7
	Spring	Single gallery	36	13.8	5.3	1.9	9.5
		B	36	23.5	14.3	5.2	35.1
		BA	36	10.9	4.9	1.4	8.3
		BI	38	1.1	.6	.1	.7
	Summer	Single gallery	36	3.4	2.4	.8	3.7
		B	36	6.2	8.8	2.3	20.8
		BA	36	2.8	2.3	.7	5.1
		BI	38	1.0	.5	.1	.6

[1] $6 \times 6 = \frac{1}{4}$ ft^2 = 232 cm^2.
[2] B = brood × (6- by 6-inch area).
BA = brood per attack on a 6- by 6-inch area.
BI = brood per inch of egg gallery on a 6- by 6-inch area.

3. Errors in estimating and identifying stages of the beetles from radiographs taken at 25 KV were less than 10 percent of the mean, thus yielding estimates acceptable for population studies of bark beetles.

4. Estimates of egg gallery length could best be taken when larvae were small because extensive mining by the time larvae are mature obscures some of the egg gallery.

5. Attack density of parent adults can be determined from radiographs taken during any stage of beetle development (Amman and Rasmussen 1969).

Techniques developed during laboratory studies were then tested under field conditions (Amman and Rasmussen 1974).

Unlike larvae of the western and southern pine beetles, which spend much of the developmental period in the outer bark, mountain pine beetle larvae in the thin bark of lodgepole pine feed and pupate primarily in the phloem layer against the sapwood surface. Consequently, removal of bark samples for radiographing would also expose larvae for direct counting. Therefore, any advantage of using the radiographic method in the field would be in the accuracy and speed of sampling beetles *in situ* and to follow the same cohort through to adult emergence.

A chain saw was used to cut two vertical slots into the trunk of each tree for film placement. This procedure resulted in a "slab" up to 2 inches (5 cm) thick, approximately 30 inches (75 cm) above ground level; slots were located at random with respect to cardinal direction. Slots were used because radiographing the entire tree would (1) superimpose images of broods from the near side upon those on the far side, (2) require a much

Table 6.—Percent of mountain pine beetle larval survival as estimated by measurement unit

Diameter class	Measurement unit[1]	Larval survival from			Average attack density per diameter class
		Fall to spring	Spring to summer	Fall to summer	
Inches		*Percent*			
9 (23 cm)	Single gallery	49.58	36.90	18.30	3.04
	B[2]	34.28	58.16	19.94	
	BA	30.11	54.37	16.37	
	BI	35.13	62.24	21.86	
12 (30.5 cm)	Single gallery	33.12	33.75	11.18	3.37
	B	25.54	71.81	18.34	
	BA	23.19	74.05	17.18	
	BI	24.91	60.56	15.09	
15 (38 cm)	Single gallery	46.57	38.38	17.87	4.04
	B	46.10	59.22	27.30	
	BA	74.98	61.10	45.81	
	BI	31.86	81.94	26.11	

[1]6 × 6 = 1/4 ft^2 = 232 cm^2.
[2]B = brood × (6- by 6-inch area).
BA = brood per attack on a 6- by 6-inch area.
BI = brood per inch of egg gallery on a 6- by 6-inch area.

greater exposure time, and (3) result in radiographs of low contrast. The slots were about 8 by 10 inches (20 by 25 cm), to accommodate film of that size in individual packets, and were open only on one side in the larger trees to slow the rate of tissue drying. In the smaller trees, the trunk was not large enough to keep one side of the slot closed; consequently, slots were open on both sides. However, all slots were sealed with caulking cord to slow the rate of drying between sample dates.

An evaluation of the radiographic method of sampling mountain pine beetle populations was based on both statistical and operational considerations. Estimates were compared with those obtained from the same trees, using the bark-removal method of Carlson and Cole (1965).

Assuming negligible location effects, no significant difference at the 0.05 level of probability was revealed among population estimates obtained by using either the bark-removal method or estimates made from radiographs for any of the three sample dates (table 7). One source of difference was noted between estimates obtained by the two methods for the first sample: eggs could be counted in bark samples, but not on radiographs. As observed previously (Amman and Rasmussen 1969), radiographing mountain pine beetles through wood precluded detection of the slight difference in density of eggs. Eggs of the western pine beetle have been seen on radiographs when only bark was radiographed (DeMars 1963). The authors detected no significant difference between methods for estimates of egg gallery nor of gallery starts. Therefore, estimates from radiographs appear to be comparable to those obtained by bark-removal sampling (Carlson and Cole 1965).

Table 7.—Comparison of estimates of mountain pine beetle brood density, gallery lengths, and gallery starts from bark-removal and radiographic sampling

	Bark-removal sampling	Radiographic sampling[1]	Significance
	Average/ft^2 (930 cm^2)		
Brood number:			
Observation 1	215.5	177.5	$P > 0.10$
Observation 2	83.2	78.3	$P > 0.10$
Observation 3	48.2	40.6	$P > 0.10$
Gallery (cm)	261.1	238.3	$P > 0.10$
Gallery starts	10.0	8.9	$P > 0.10$

[1]Estimates made by two observers were averaged and the average was compared with the estimates obtained by bark-removal sampling.

Comparisons of estimates made from radiographs by the two observers revealed no significant difference for beetle populations and egg gallery (table 8). However, the observers gave significantly different estimates for the numbers of gallery starts ($P<0.01$). Overall, observer differences were small, and adequately trained observers can be expected to give comparable estimates from radiographs.

The bark-removal method was almost 2.5 times faster than the radiographic method. Costs were proportional to time—$1 per sample using the bark-removal method and $2.50 per sample using the radiographic method (1974 costs).

A major disadvantage of the radiographic method was the inability to assess mortality from the radiographs. Some predators could be seen and counted on the radiographs. The only one of consequence was *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae). Dead beetles that had dried completely were not often detected; usually those that were could not be assigned to specific causes of mortality. In addition, larvae that had died recently but still contained much moisture could not be distinguished from living larvae. The bark-removal sampling technique is definitely superior in this respect, because the cause of death of most larvae can be determined. Consequently, the bark-removal sampling method will continue to be the choice for life table sampling of mountain pine beetles in lodgepole pine where assessment of mortality factors is of primary concern.

MODELING

A mathematical model should contain the essential relations under study. The success of the model depends upon whether those factors included are really essential to the explanation. Biological entities are so complex that it is impossible to choose more than a fraction of all factors for study. The study of a few carefully selected factors can lead to improved understanding of the relations under study and provide leads for subsequent investigations. However, the study of too few factors for too short a time can lead to misinterpretations. Conceptual or theoretical models give clues to modes of behavioral interactions and may point toward important population characteristics. Empirical models give an accounting of these facets. In either case, if the model is to be used as a measurement tool, the nature or mode of operation of the biological unit must be thoroughly understood to correctly interpret these components in terms of population dynamics.

Models are simplifications of reality. A model, however simple, should be an accurate representation of that reality. Were it to be complete in every detail, it then would be equivalent to real life. Ultimately, it is the closeness of agreement between the model and the real system—the validation of the model—that determines its usefulness. It is futile and useless to test the model with data used in its construction or to conceptualize without verification. Only through further experimentation can discrepancies between predicted and measured behavior be resolved or minimized.

Both conceptual and predictive models are found in mountain pine beetle literature. Models discussed here will be limited to those not previously discussed in parts I and II of this monograph on mountain pine beetle. Parts I and II contain most of the two- and three-dimensional models of beetle, host, or beetle-host interactions.

The models in this publication have to do with the interactions of stands and beetle populations and are presented in an order consistent with the life cycle of the beetle.

Beetle Life Table Models

The life table is one of the oldest, most useful, and best known expressions in the field of population studies. Deevey (1947) defined it as succinctly and clearly as anyone: "A life table is a concise summary of certain vital statistics of a population." Therefore, the life table approach was used to determine the principal factors affecting natality and mortality of mountain pine beetle.

The life tables were based on intensive population sampling from annually established plots within both high and low level populations of the beetle. These data have been supplemented with detailed studies in both field and laboratory.

Data for life tables.—The observation times and the types of data collected were:

1. N_E = egg density. This is the first observation taken when the flight and attack period of the parent adult beetle is reasonably completed and the majority of egg deposition accomplished. The data needed from this observation are number of attacks, number of egg niches and larval starts, number of small larvae, and length of egg gallery.

Table 8.—Comparison of observer estimates of mountain pine beetle brood densities, gallery lengths, and gallery starts made independently from the same set of radiographs

	Observer 1	Observer 2	Significance
	Average ft² (930 cm²)		
Brood number:			
Observation 1	171.5	183.5	$P > 0.05$
Observation 2	82.9	73.6	$P > 0.10$
Observation 3	45.2	36.0	$P > 0.10$
Gallery (cm)	234.4	242.1	$P > 0.10$
Gallery starts	6.3	11.5	$P < 0.01$

2. N_1 = brood density prior to winter. This observation is taken as close to the onset of winter as possible. Data from this observation should include additional attacks and egg deposition and small larvae density.

3. N_2 = brood density immediately postwinter (April). This observation determines winter kill and includes both small and possibly large larvae density.

4. N_3 = late spring brood density (May). Data will include small and large larvae and possibly pupae densities. This and N_4 are the more important observations. If critical population changes occur, they will begin to show during these stages.

5. N_4 = early summer brood density (June). The description of N_3 suffices for this observation.

6. N_5 = late summer brood density (July). Large larvae, pupae, and callow adult densities are included.

7. N_{na} = emerging new adults. This observation is a sample of emerging adults and represents brood survival. The caging can be done at any time after N_4 and prior to flight.

These seven observations are probably the ideal for a complete life table. However, we found suitable life tables could be constructed by combining and omitting observations. We settled on the following observations:

1. Late fall: The population surviving the egg stage and entering the winter period as second and third instar larvae ($N_E + N_1$).
2. Spring: The population surviving winter and containing the third and fourth instar larvae (N_2).
3. Summer: The population containing the mature larvae and pupae ($N_3 + N_4 + N_5$).
4. Emerging adults: The final surviving population estimates of emerging adults obtained by caging a 6- by 6-inch (232-cm^2) area of bark (N_{na}).

Using life tables.—Life tables can demonstrate population trend. Examples of decreasing and increasing populations are shown in tables 9 and 10. The importance of N_3 and N_4 is shown in comparison of M_x (mortality occurring during interval x) for these respective age intervals. If, during N_3, the brood loss due to MF_2 (mortality factor in interval 2) increases only 0.85 larva, this can be great enough to almost halve the loss due to MF_4 (say, competition). In other words, a so-called beneficial predator could reduce the pressure from competition to the

Table 9.—Life table for a mountain pine beetle population showing a decreasing trend

x	N_x	M_xF		M_x	100 M/N
Age-interval	No. alive at start of x	Factor responsible for M_x		No. dying during x	M_x as percentage of N_x
N_o – adults	1 female				
N_E – eggs	100.00	MF_1		23.63	23.63
		MF_2		16.84	16.84
		MF_3		6.78	6.78
			Total	47.25	47.25
N_1 – small larvae	52.75	MF_1		8.25	15.64
		MF_2		3.00	5.69
		MF_4		20.00	37.91
		MF_3		1.00	1.90
			Total	32.25	61.14
N_2 – small larvae	20.50	MF_5		12.13	59.17
N_3 – large larvae	8.38	MF_2		1.15	13.72
		MF_4		5.03	60.02
		MF_3		.45	5.37
			Total	6.63	79.11
N_4 – large larvae	1.75	MF_2		0.25	14.28
pupae		MF_1		.15	8.57
		MF_4		.05	2.86
		MF_3		.05	2.86
			Total	0.50	28.57
N_5 – pupae	1.25	MF_2		0.35	28.00
callow adults		MF_1		.30	24.00
		MF_3		.10	8.00
			Total	0.75	60.00
N_{na} – new adults	0.50	Brood mortality			99.50
females	.25	Generation mortality			75.00 (–)
N_{E+1}	25.00				

Table 10.—Life table for a mountain pine beetle population showing an increasing trend

x	N_x	M_xF		M_x	100 M/N
Age-interval	No. alive at start of x	Factor responsible for M_x		No. dying during x	M_x as percentage of N_x
N_0 – adults	1 female				
N_E – eggs	100.00	MF_1		23.63	23.63
		MF_2		16.84	16.84
		MF_3		6.78	6.78
			Total	47.25	47.25
N_1 – small larvae	52.75	MF_1		8.25	15.64
		MF_2		3.00	5.69
		MF_4		20.00	37.91
		MF_3		1.00	1.90
			Total	32.25	61.14
N_2 – small larvae	20.50	MF_5		12.13	59.17
N_3 – large larvae	8.38	MF_2		2.00	23.87
		MF_4		2.80	33.41
		MF_3		.45	5.37
			Total	5.25	62.65
N_4 – large larvae	3.13	MF_2		0.10	3.19
pupae		MF_1		.07	2.24
		MF_4		.07	2.24
		MF_3		.01	.32
			Total	0.25	7.99
N_5 – pupae	2.88	MF_2		0.17	5.90
callow adults		MF_1		.15	5.21
		MF_3		.06	2.08
			Total	0.38	13.19
N_{na} – new adults	2.50	Brood mortality			97.50
females	1.25	Generation mortality			25.00 (+)
N_{E+1}	125.00				

extent that the population is released, and this in effect causes an increase in the generation trend. The end effect is an increase of 25 percent more female beetles emerging than attacked. This also points out the importance of caging for emerging adults to obtain the generation trend. Brood mortality differed by only 2 percent, yet generation mortality differed 100 percent. Five times more adult female beetles emerged in the second situation than in the first.

An additional column, S_x (survival rate within x), can be added to the life table at this time. The use of survivals rather than mortalities presents a more reasonable approach because it is the residual live populations that concern us most. An example is shown in table 11.

The accumulated life tables can now be used in a mathematical model to describe and define the causes of change. The analysis of the model is based on the age-interval survival rates (Morris 1963).

The model follows the form:

$$S_G = S_E \times S_1 \times S_2 \times S_3 \times S_4 \times S_5 \times P_F \quad (1)$$

where

N = population density of the mountain pine beetle per 0.25 ft^2 of bark area.

N_E, N_1 . . . N_3, N_{na}, N_{pa} represent eggs, brood density by each of five observations, new adults and parent adults, respectively.

S_E = survival of eggs to eclosion = N_1/N_E.

S_1 = fall survival of brood from observation 1 to observation 2 = N_2/N_1.

S_2 = winter survival of brood = N_3/N_2.

S_3 = late spring survival of brood = N_4/N_3.

S_4 = early summer survival of brood = N_5/N_4.

S_5 = late summer survival of brood = N_{na}/N_5.

P_F = the average proportion of fecundity of the adult female population at the current attack density; extent of egg deposition is inversely proportional to attack density.

S_G = survival in any generation (equation 1).

Table 11.—Survival rates for mountain pine beetles and computed generation survival estimated from tables 9 and 10

Life table	x Age-interval	No. alive at start of x	N_{x+1}/N_x	S_x Survival rate within x
1	N_E	100.00	N_1/N_E	0.528
	N_1	52.75	N_2/N_1	.389
	N_2	20.50	N_3/N_2	.409
	N_3	8.38	N_4/N_3	.209
	N_4	1.75	N_5/N_4	.714
	N_5	1.25	N_{na}/N_5	.400
	N_{na}	.50		$S_G = 0.005$
2	N_E	100.00		0.528
	N_1	52.75		.389
	N_2	20.50		.409
	N_3	8.38		.374
	N_4	3.13		.920
	N_5	2.88		.868
	N_{na}	2.50		$S_G = 0.025$

Simple regressions are used and examples of their statistics are listed in table 12. S_G is the dependent variable and the terms S_E . . . P_F independent variables. Transformation of the data, S_E . . . P_F, to common logs is necessary to provide for a linear additive model. The data are also coded by 10,000 to avoid negative logarithms. Thus, equation 1 becomes:

$$\text{Log } 10{,}000\ S_G = \text{Log } 10{,}000\ S_E + \ldots + \text{Log } 10{,}000\ P_7 \quad (2)$$

The regressions are used to determine whether survival in any age interval is a key to determining generation survival. If such occurs, then prediction of S_G can be possible from sampling the age interval(s) responsible for S_G. It follows then, to explain variation in S_G, we must explain the variation in the age interval(s) most responsible for that variation in S_G.

The determination of the variation within S_3 and S_4 could be the next step. Meanwhile, correlations and regressions can be computed for age intervals and generation survivals and for the parasite-predators within their respective age intervals. The latter regression can be used to determine which, if any, biotic agents are causing the variations, thus improving the evaluation of an infestation by explaining and predicting its trend and recommending the application and timing of control measures.

Table 12.—Example of regression statistics for a mountain pine beetle generation survival model. Mean survival for observation, $\bar{x}$; coefficient of determination, r^2; correlation coefficient, r; intercept, a; slope, b (scaled by 10,000)

Area	Observation	$\bar{x}$	r^2	r	a	b
Wasatch	S_E	0.521	0.004	−0.06	2.44	−0.18
	S_1	.197	.457	−.68	4.98	−.97
	S_2	.492	.021	.14	1.07	.20
	S_3	.871	.967	.98	−1.20	.75
	S_4	.355	.999	−.99	5.29	−.99
	S_5	.834	1.000	1.00	−3.33	1.30
	P_F	.458	.723	.85	−7.42	2.51
	(S_G = 0.005964)					
Teton	S_E	.621	.741	−.86	29.04	−7.11
	S_1	.425	.940	.97	.79	.36
	S_2	.461	.955	.98	.84	.34
	S_3	.696	.332	.58	−3.20	1.38
	S_4	1.965	.921	−.96	22.83	−4.83
	S_5	.216	.918	−.96	10.67	−2.57
	P_F	.337	.000	−.01	2.57	.14
	(S_G = 0.012113)					

During the last 2 of the 3 years of study, the mountain pine beetle parent adult female either elongated the egg gallery and resumed egg deposition, or emerged, flew, and reattacked infested trees, attacked new trees, or both. This phenomenon was more pronounced and in greater consequence on the Teton plots (S_4 $\bar{x}$ = 1.965) than on the Wasatch plots (S_3 $\bar{x}$ = 0.871). The addition of new brood (almost double) halfway through the life cycle overcame the effect of the reduction factors to the extent the number of emerging adults was almost equal to the number of eggs deposited in S_E. Consequently, the correlation coefficients are high for the Teton, S_E . . . S_5.

An analysis of variance was done to compare the effects of plots and year (table 13).

Table 13.—Variance of mountain pine beetle survival in each age-interval. Plot and year are main sources of variation (transformed data)

Survival	Source of variation	Both plots	Wasatch	Teton
S_E	Plots	0.00877		
	Years	.00648	0.02171	0.017830
S_1	Plots	.16616		
	Years	.00055	.08691	.016507
S_2	Plots	.00117		
	Years	.34743	.10303	.149240
S_3	Plots	.01427		
	Years	.01707	.30640	.212630
S_4	Plots	.83865		
	Years	.10859	.18339	.047950
S_5	Plots	.51536		
	Years	.13860	.11429	.168470
P_F	Plots	.02656		
	Years	.04917	.02082	.013460
S_G	Plots	.14950		
	Years	.90938	.18203	1.214610

The Wasatch infestation was, in fact, decreasing with respect to number of host trees infested each year. However, attack density and egg deposition were greater on the Wasatch than on the Teton plots. The mortality within any one generation had been as expected for the Wasatch (decreasing trend), but for the Teton (explosively increasing), the generation mortality percentage had been less than the survival percentage (more adults emerging than attacked) (table 14).

For either infestation, the greatest variation in SG is probably to S_3 or S_4 (table 12). Hence, these are the observation times for intensive work to determine factors of change. Inferences from table 13 are:

S_E . . . S_2 —Small, consistent, or low magnitude contributed variance, except S_2 between years. This is due to the catastrophic winter kill during 1962, Teton (table 14).

S_3 —Contributed variance of little consequence. However, resumption of attacks and egg deposition probably obscured the real magnitude.

S_4 and S_5 —Reattacks and egg deposition in full activity and more pronounced on the Teton. Thus, the higher contributed variance by plots.

P_F —Fecundity remained fairly constant for sources concerned.

Some correlations between parasite-predator densities and age-interval survivals were computed. For most parasite-predator groups the correlation coefficients remained stable for each age interval. However, for *Medetera* the correlation was quite low except for the Wasatch S_4 where the degree of correlation increased slightly. In this situation, the Wasatch had consistently shown a higher percentage of *Medetera*. The age interval S_4 had been the point of separation between the two populations with respect to generation mortality/survival ratios.

The analysis of age-interval survivals in relation to generation survival had certain preliminary value and gave considerable insight during the early stages of our research.

Abridged cohort life tables.—The abridged cohort life table, in which a generation of beetles is sampled at particular points in time, was used thereafter in this study (Chiang 1968). In its strictest form, a cohort life table is a record of the actual mortality experienced by a given group of individuals over a period extending from birth of all individuals until death of the last member of that group. However, death of the last member in this case was not necessarily recorded. Rather, the emergence of

Table 14.—Comparison of mountain pine beetle population trends for attack density and egg deposition per square foot of bark, and mortality and survival percents by years at two locations

Area	Year	Attack density	Egg deposition	Mortality (−) survival (+)	
				Egg to adult	Adult to adult
				Percent	
Wasatch	1961	28.1	800	99(−)	89(−)
	1962	24.0	1,035	94(−)	63(−)
	1963	16.0	1,027	97(−)	73(−)
Teton	1961	14.1	306	69(−)	225(+)
	1962	15.0	545	[1]99(−)	[1]98(−)
	1963	15.0	598	71(−)	278(+)

[1]Catastrophic winter kill—highly localized over plot area.

the adult beetle was equated as the end of life for that particular cohort. Thus, mortality during the flight period was not recorded.

The ideas and procedures used in the construction of the abridged cohort life table are the same as those used in the construction of the complete life table except for differences that result from the length of intervals.

Table 15, an example of an abridged cohort life table used, is explained in detail:

Column 1. Diameter at breast height (d.b.h.) for three groups of trees in which mountain pine beetle were sampled. Observation numbers correspond to: 1 is early fall; 2 is late fall; 3 is early spring; 4 is early summer; and 5 is late summer (newly emerged adults).

Column 2. Age interval (x_i to x_{i+1}). Each interval is defined by the two ages stated except for the final age interval, which ends with the emergence of the adult beetle.

Column 3. Number alive at age x_i, l_i. Totaling the number alive, dead, and for all stages gives a base population, l_0. Thereafter, survivors per sampling time will comprise l_i.

Column 4. Number dying in interval (x_i to x_{i+1}), d_i. These are the actual counts of dead individuals at the time of sampling. The number dying is derived by subtraction: $l_i - l_{i+1}$. If actual counts are used, then sampling error must be taken into account; high sampling errors can be the reason for an apparent increase in population from l_i to l_{i+1}.

Column 5. Proportion dying in interval (x_i to x_{i+1}), $\hat{q}_i$. Each $\hat{q}_i$ is an estimate of the probability that an individual alive at the age x will die during the interval (x_i to x_{i+1}). $q_i = \frac{d_i}{l_i}$

Column 6. Proportion surviving in interval (x_i to x_{i+1}), p_i. Each p_i is an estimate of the probability that an individual alive at age x will survive during the interval (x_i to x_{i+1}). $\hat{p}_i = 1 - \hat{q}_i$.

Column 7. Variance of proportion dying during the interval is equal to the variance of proportion surviving during the interval.

Column 8. The length of the typical ith interval in this particular abridged life table is dependent upon the sampling interval, which is neither uniform in length for all intervals nor longer than a few months. The essential element here is the average fraction of the interval lived by each beetle that dies at an age included in the interval. This fraction is denoted by a_i. The assumption of $a_i = 0.5$ for each time unit of age within an interval (x_i to x_{i+1}) does not necessarily imply that $a_i = 0.5$ for the entire interval. The value of the fraction a_i depends on the mortality pattern over an entire interval, but not on the mortality rate for any single generation. When the mortality rate increases with age in an interval, the fraction $a_i > 0.5$; when the reverse pattern prevails, $a_i < 0.5$. In our particular case, the fraction a_i was necessarily taken to be 0.5 of the sampling interval, because time of death within the sampling interval or interval lived was not measured.

Column 9. Number of time units lived in interval (x_i to x_{i+1}), L_i. Each member of the cohort who survives the interval (one generation year) contributes one interval to L_i, while each member who dies during the interval contributes, on the average, a fraction a_i of that interval where a_i is assumed to be 0.5.

$L_i = n_i (l_i - 0.5\ d_i)$

Table 15.—Example of an abridged cohort life table for mountain pine beetle. Detailed descriptions are in text

1	2	3	4	5	6	7	8	9	10	11	12
D.b.h./ obs.	Age interval (days)	No. living at age x_i	No. dying during interval	Proportion dying during interval	Proportion surviving interval	$V_{q_i} = V_{p_i}$	Average fraction of last age interval	Number of time units lived in interval	Total time units lived beyond age x_i	Obs. E (life) at age x_i	S.E. e_i
	x_i to x_{i+1}	l_i	d_i	q_i	P_i		a_i	L_i	T_i	e_i	
23 cm											
1	30	3,079	325	0.1056	0.8944	0.000031	0.50	87,495	633,540	212.748	1.450
2	180	2,754	958	.3479	.6521	.000082	.50	409,500	546,045	206.084	.997
3	60	1,796	676	.3764	.6263	.000131	.50	87,480	136,545	88.004	.906
4	30	1,120	403	.3598	.6402	.000206	.50	27,555	49,065	63.013	.868
5	60	717	717	1.0000	0		.50	21,510	21,510	60.000	0
30 cm											
1	30	3,309	633	.1913	.8087	0.000047	0.50	89,775	600,345	187.937	1.609
2	180	2,676	1,074	.4013	.5987	.000090	.50	385,020	510,570	198.845	1.058
3	60	1,602	598	.3733	.6267	.000146	.50	78,180	125,550	91.816	.995
4	30	1,104	286	.2849	.7151	.000203	.50	25,830	47,370	68.635	.862
5	60	718	718	1.0000	0		.50	21,540	21,540	60.000	0
38 cm											
1	30	2,936	670	.2282	.7718	0.000060	0.50	78,030	523,600	184.363	1.804
2	180	2,266	815	.3598	.6403	.000102	.50	334,530	445,570	204.440	1.110
3	60	1,451	546	.3763	.6237	.000162	.50	70,780	111,040	88.718	1.016
4	30	905	312	.3448	.6552	.000250	.50	22,470	40,260	64.144	.958
5	60	593	593	1.0000	0		.50	17,790	17,790	60.000	0

Column 10. Total number of time units lived beyond age x_i, T_i. This total is equal to the sum of the number of time units lived in each age interval beginning with age x.

$$T_i = L_i + L_{i+1} + L_{i+2} + \ldots + L_w$$

Column 11. Observed expectation of life at age x_i, $\hat{e}_i$. This is the average number of time units yet to be lived by an individual now age x_i. Because the total number of time units of life remaining to the l_i individuals is T_i,

$$e_i = \frac{T_i}{l_i}, \quad i = 0, 1, \ldots, w$$

Each $\hat{e}_i$ summarizes the mortality experience of individuals beyond age x_i in the cohort population under consideration, making this column very important in the life table. Furthermore, this is the only column in the table other than q_i and a_i that is meaningful without reference to the starting population, l_0. As a rule, the expectation of life, $\hat{e}_i$, decreases as the age, x_i, increases (with the single exception of the first interval of life, when the reverse is true due to high mortality during that interval). The symbol, $\hat{e}_i$, denoting the observed expectation of life, is computed from the actual mortality data and is an estimate of $\hat{e}_i$, the true unknown expectation of life at age x_i.

Column 12. Sampling error of life expectation at age x_i.

Sample variance of (1) the proportion $\hat{q}_i$ of individuals dying in an interval (x_i, x_{i+1}), (2) the proportion $\hat{p}_{ij}$ of individuals alive at age x_i who will survive to age x_j, and (3) the observed expectation of life $\hat{e}_\alpha$, at age x_α, can be computed in the following manner:

In a cohort life table, the proportions $\hat{q}_i$ and $\hat{p}_i$ are computed directly from

$$\hat{q}_i = \frac{d_i}{l_i} \text{ and } \hat{p}_i = \frac{l_i + 1}{l_i}$$

and are ordinary binomial proportions with the sample variance

$$S\hat{p}_i^2 = \frac{l}{l_i}[p_i q_i]$$

The proportion $\hat{p}_{ij}$ of survivors is a general form of $\hat{p}_i$ and is equal to $\hat{p}_i$ when $j = i+1$. Corresponding to the sample variance of $\hat{p}_{ij}$ is

$$S^2\hat{p}_{ij} = \frac{l}{l_i}[\hat{p}_{ij}(1 - \hat{p}_{ij})], \quad i>j, \; j = 0, 1, \ldots n$$

The $\hat{p}_i$'s are linearly uncorrelated, and therefore the sample variance of $\hat{p}_{ij}$ also has the form

$$S^2\hat{p}_{ij} = \hat{p}_{ij}^2 \sum_{h=i}^{j-1} \hat{p}_h^{-2} \; S\hat{p}_h^2$$

Let Y denote the future lifetime of an individual at age x_α; the observed expectation of life $\hat{e}_\alpha$ is simply the same mean $\overline{Y}_\alpha$ of the l_α values of Y, or

$$\hat{e}_\alpha = \overline{Y}_\alpha$$

These values of Y are recorded in the life table in the form of a frequency distribution in which d_i is the frequency in the interval (x_i, x_{i+1}), $i = \alpha, \alpha+1, \ldots, w$. On the average, each of the d_i individuals lives x_i time units plus a fraction of α_i of the interval (x_i, x_{i+1}), or $x_i - x_\alpha + \alpha_i n_i$ time units beyond x_α; that is, for each of the d_i individuals,

$$Y_\alpha = x_i - x_\alpha + \alpha_i n_i, \quad i = \alpha, \alpha+1, \ldots, w$$

In this case, n_i is the length of the typical ith interval in an abridged table, or $n_i = x_{i+1} - x_i$, which is greater than one time unit.

The sample mean of Y_α can then be expressed as

$$\hat{e}_\alpha = \overline{Y}_\alpha = \frac{1}{l_\alpha} \sum_{i=\alpha}^{w} (x_i - x_\alpha + \alpha_i n_i) d_i$$

and the sample variance of Y_α as

$$S^2Y_\alpha = \frac{1}{l_\alpha} \sum_{i=\alpha}^{w} [(x_i - x_\alpha + \alpha_i n_i) - \hat{e}_\alpha]^2 d_i$$

Therefore, the sample variance of the sample mean $\overline{Y}_\alpha$, or $\hat{e}_\alpha$, is given by

$$S\hat{e}_\alpha^2 = \frac{1}{l_\alpha} \; S^2Y_\alpha$$

or

$$S\hat{e}_\alpha^2 = \frac{1}{l_\alpha^2} \sum_{i=\alpha}^{w} [(x_i - x_\alpha + \alpha_i n_i) - \hat{e}_\alpha]^2 d_i$$

Beetle Life Stage Models

Using data obtained by sampling for life tables, survival of the various beetle stages was modeled in relation to lodgepole pine size, from endemic through the epidemic and postepidemic stages. Later, these data were linked by life stage to stand characteristics and stand mortality. These models portray smoothed insect density trends over years by life stage and size of infested tree.

Data analysis consisted of plotting brood densities for each life stage over d.b.h. of the infested tree and observed year of the infestation. Data are presented on the basis of diameter rather than phloem thickness, the main determinant of mountain pine beetle brood production, because much of the data through the main years of the epidemic were taken before recognition of the importance of phloem thickness. However, the relation of phloem to diameter is firmly established (Amman 1969, 1975, 1978; D. M. Cole 1973). Trends smoothed in accord with expectation over both d.b.h. and year were established through these points. The resulting surfaces were described mathematically using techniques presented by Jensen and Homeyer (1970, 1971) and Jensen (1973). The appendix contains FORTRAN statements of the mathematical descriptions (Cole and others 1976).

Each model was first developed graphically using expectation, known constraints, and apparent data trends in arriving at smoothed curve forms. These were fitted through the data by approximate "least deviations." The resulting graphic forms were described algebraically. These descriptors were given a simple adjustment (<5 percent in all cases) to their respective data sets that consisted of the ratio of the sum of the descriptor values for the observations to the sum of the actual values.

Eggs.—Within any year of the infestation, egg density increased with diameter. This positive relation was weakly displayed in years 3 to 6 and more strongly displayed in years 7 to 12 (fig. 1A). This was the net result of more attacks and related increased oviposition in the

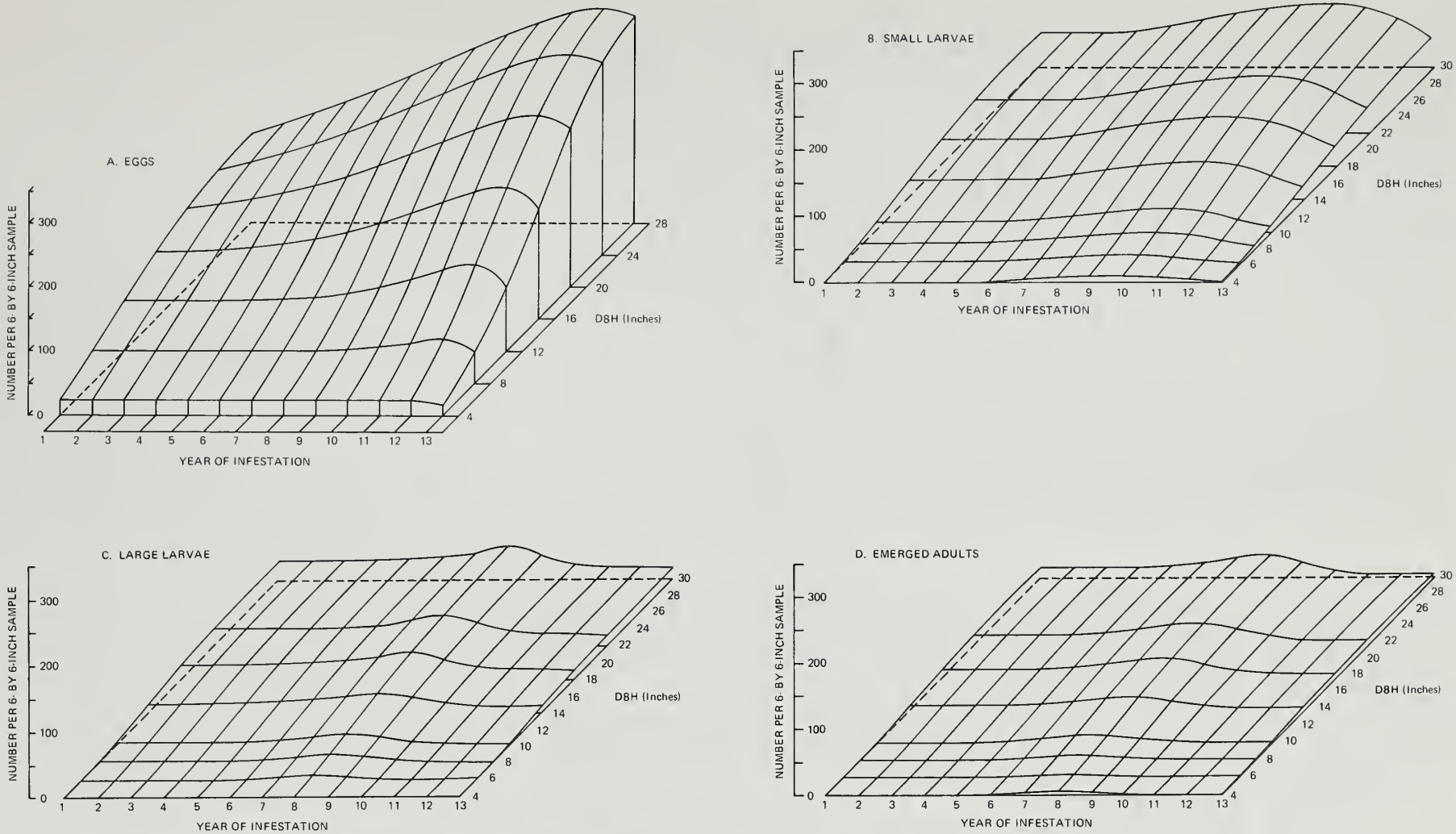


Figure 1.—Densities of four life stages of the mountain pine beetle by tree diameter for 13 years. A. Eggs; B. small larvae; C. large larvae; D. emerged adults (Cole and others 1976).

larger thick-phloem trees early in the epidemic. Of particular interest was the increase in egg density beyond the peak year of emergence (year 8). Apparently, the population and attack density remains high past the peak of the epidemic. Egg density declined slightly in year 13, about 3 years after emergence had returned to the endemic level. Beetles attack fewer trees but at a greater density (Klein and others 1978) following the peak of the epidemic.

Small larvae.—Survival of small larvae through the winter (fig. 1B) also increased with diameter and peaked in the 10th year, 2 years before peak egg deposition. This positive d.b.h. effect existed in all but year 12, and in about half of those years the effect was weak. The negative effect in year 12 was strong. However, the bulk of evidence indicated a positive d.b.h. effect, and this was imposed on year 12, also. The decline in survival that starts with the 11th year probably is related to intraspecific larval competition (within broods) that continues to intensify as egg gallery starts and inches increase with years (fig. 2).

Large larvae.—Survival in the large larval stage (fig. 1C) peaked in year 8, which was 2 years before the peak of small larvae. Large larval survival was relatively steady from year to year within all diameter classes during the endemic period (years 1 to 5). However, survival increased substantially in years 6 to 8.

Low density of large larvae occurs during the endemic years, the result of low levels of attack and gallery density; hence, low density of eggs laid per unit of bark (fig. 1A). Laboratory studies demonstrated that beetle emergence is directly related to inches of egg gallery when phloem is underutilized (fig. 3; Amman 1972). As the infestation progresses and egg galleries increase, an apparent optimum is reached when maximum numbers of large larvae per unit of phloem occur (year 8). After year 8, increased competition among larvae (between galleries), but particularly increased drying, probably causes reduced survival. Increases in attack density and egg gallery density do not cause a decline in beetle survival per unit area for any given phloem thickness in the laboratory when material remains moist throughout beetle development (Amman and Pace 1976). However, in the field, construction of egg galleries promotes drying of the phloem, especially when gallery density is high. Drying also is enhanced by large numbers of feeding larvae as they exhaust the available phloem.

Adults.—Adult density trends are similar to those of large larvae, but at a reduced level, with the peak still occurring in year 8 (fig. 1D). When development reaches the large larval stage, a high probability exists that larvae will also reach the adult stage. Final emergence was highly correlated with numbers of individuals in the large larval stage. Emergence within a diameter class was fairly steady during the endemic period (years 1 to 5) but was greater in large diameter trees.

The transition of the infestation from endemic to epidemic is dependent upon successful infestation of large trees, where beetle production per parent is high (fig. 4). Toward the latter years of the epidemic (years 11 to 13), only large trees, on the average, could be expected to produce enough brood to keep the infestation going. However, by this time, few such trees remain in a stand.

Mortality factors acting on mountain pine beetle populations have been evaluated (Cole 1974, 1981). However, none of these appear to regulate the beetle population at a level that saves trees. An epidemic runs its course, killing most of the large diameter trees, then declines when beetles have only small diameter trees to infest. Beetles must either emigrate from the stand (Klein and others 1978) or infest the small remaining trees in which brood production is low because of thin phloem and excessive drying during beetle development. Therefore, the strong expectation for a positive d.b.h. effect appears correct when considering tree mortality and brood density. These have been reasonably well established by both laboratory and field work.

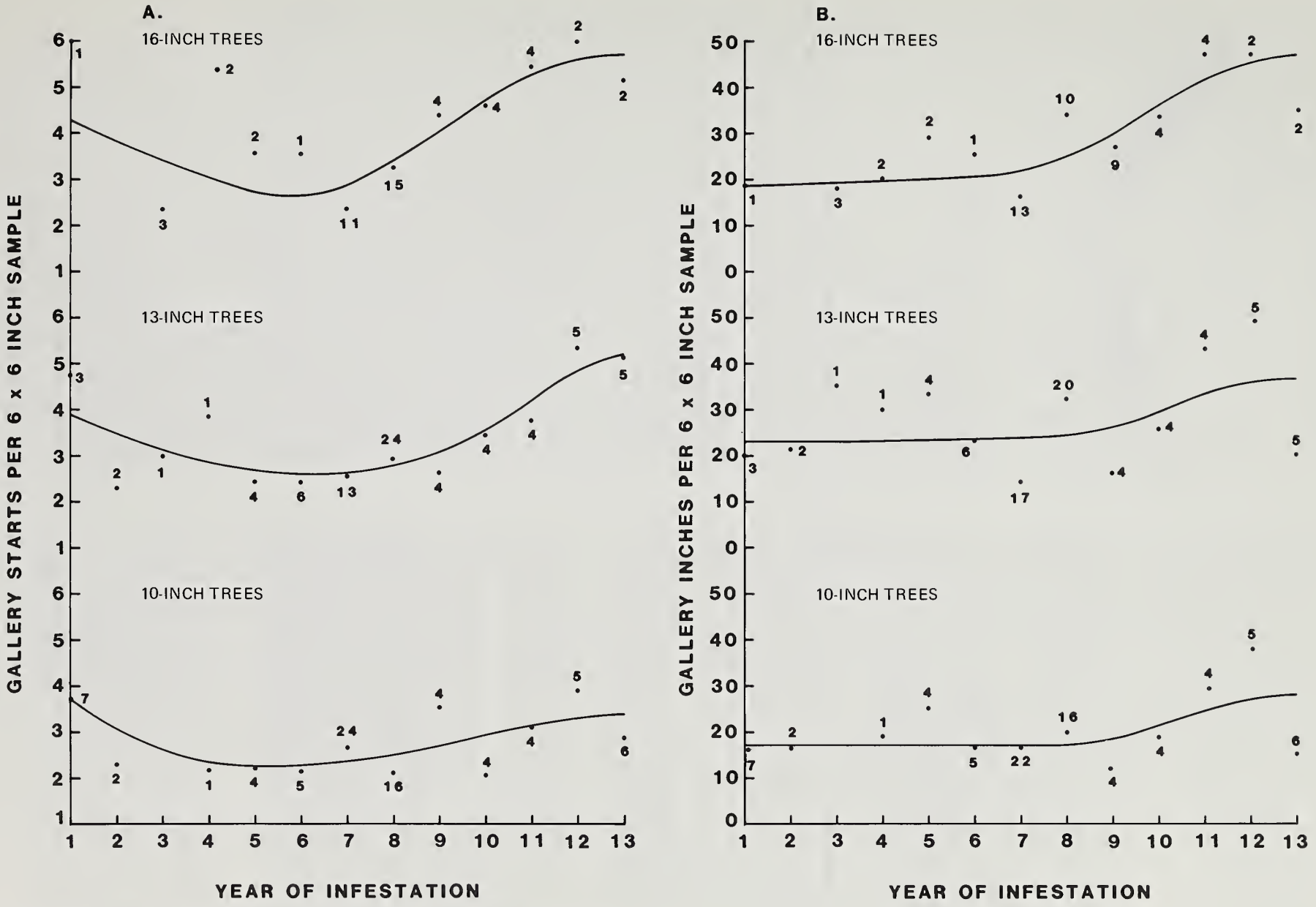


Figure 2.—Mountain pine beetle egg gallery starts and length of egg gallery by diameter for 13 years. A. Egg gallery starts; B. egg gallery inches. Number at each data point indicates number of trees sampled (Cole and others 1976).

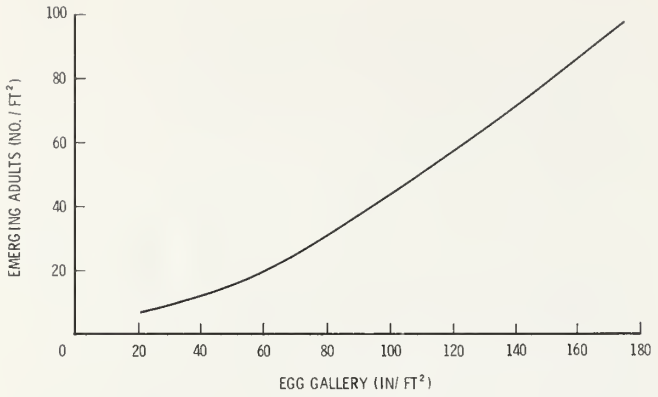


Figure 3.—Relation between number of emerging brood adults of the mountain pine beetle and inches of egg gallery made by parent adults in thick phloem (0.16 to 0.26 inch or 4.1 to 6.6 mm thick; $\hat{y} = 3.26 + 0.0408 (x^{1.5})$; $s_{y \cdot x} = 24$; $r^2 = 0.52$) (Amman 1972).

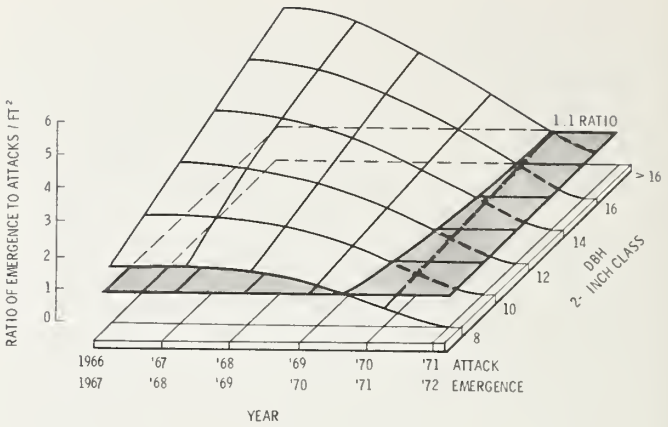


Figure 4.—Ratio of emergence to attack densities by 2-inch (5.1-cm) diameter classes during a mountain pine beetle epidemic (Klein and others 1978).

Beetle Dispersion and Aggregation Models

Upon completion of development, most of the new mountain pine beetle adults emerge in late July and early August. They disperse and, when a green tree is attacked by one or a few beetles, the aggregation pheromone is released that attracts many beetles for a mass attack of the tree.

Dispersion/aggregation model.—Burnell (1977) devised an elegant model that disperses the beetles based on a random distribution that, one could argue, is a rarity in nature. He used three assumptions in dispersal/aggregation:

1. Pioneer beetles attack with random distribution over the available bark surface.
2. A tree has a threshold of aggregation that is required to induce aggregation.
3. Any tree becoming an aggregator will be mass attacked and killed.

He assumed the tree surface areas are measured in equivalent units. Then the pioneer beetle attack density per unit could be estimated using the Poisson distribution function, and the probability of having one or more pioneer beetles attack could be calculated. The threshold of aggregation was estimated based on the number of square units of the tree that must be attacked by one or more pioneer beetles to induce aggregation. Thus, the probability of the tree becoming an aggregator could be calculated.

The mortality prediction model assumed that the threshold of aggregation is uniform across both diameter and years within an epidemic. Thus, surface killed was estimated for the stand. However, for each year, the predicted surface area mortality was forced to be the same as that observed by adjusting the pioneer beetle attack density. Therefore, using Burnell's (1977) equation to determine the threshold of aggregation minimizes the difference between predicted and residual stands.

Burnell determined the thresholds of aggregation for four plots. One plot, Hell Roaring Creek, with a rather high threshold of aggregation but also high attack densities and host resinosis, was interpreted as being more resistant to attack than the other stands. Burnell interpreted this as a stand resistance measure. However, subsequent years of infestation proved this incorrect as large numbers of trees were killed.

Burnell's model shows that in the early part of the epidemic the pioneer density is low and the comparative probability of large tree mortality versus small tree mortality is large. As the epidemic progresses, pioneer density rises and smaller trees are attacked because of this and the depletion of larger trees. Toward the end of the epidemic, pioneer beetle density decreases because emergence from infested trees declines and, as a result, the epidemic collapses. However, data taken from many epidemics (Cole and others 1976) show that gallery starts (the positive results of attack densities) are greater in the early stages of an epidemic (fig. 2), decreasing in the midyears, and increasing again in the latter years.

Aggregation/susceptibility model.—Geiszler and others (1980) developed a mathematical model to (1) describe beetle aggregation and (2) predict the relation of tree susceptibility and switching to changes in beetle density. The term "switching" is defined as the phenomenon of incoming beetles attacking an adjacent recipient tree after the focus (first) tree had been attacked by the first-arriving beetle. This receipient tree is quickly mass-attacked and killed more readily than the focus tree. These authors found that, when switching occurs, the beetles usually attack trees with a diameter greater than the average in the stand. This then enhances beetle survival because larger trees usually have thick phloem. There are at least three other conceptual models describing the switching process of attacking bark beetles. Geiszler and others (1980) labeled them as:

1. Passive model when the signal to switch is due to lack of resin exudation (Renwick and Vité 1970).

2. Threshold model when the attractive pheromone, trans-verbenol, is assumed to be the cause of switching (Coster and Gara 1968).

3. Repelling model when both trans-verbenol and a repelling pheromone reach concentrations that cause switching (Rudinsky and others 1974).

In developing the Geiszler and others model to describe daily number of beetle attacks on the lower 7.9 ft (2.4 m) of a single tree, primary factors assumed to control the attack pattern were attraction, repellence, and host factors that affect successful beetle colonization. Attraction was assumed to depend primarily upon the amount of attractant released, the population density of flying beetles, and meteorological conditions. Attraction was then modeled, based upon the amount and emission rate of trans-verbenol for 2 days. Repellence was modeled on the assumption that the repellent concentration increased linearly with the cumulative number of attacks. Resistance, by the tree, to aggregation was modeled by determining the number of unsuccessful attacks each day of the study. Thus, the main factors of aggregation were accounted for and the temporal pattern of attack was modeled. This model was then used to simulate the daily and cumulative number of attacks on the focus tree.

The attraction coefficient values varied, suggesting that (1) each tree's attractive qualities were different, (2) the local beetle population density at each tree's site was different and compensated for by adjusting the attractant and coefficient, or (3) both. Repellence also varied and was positively correlated with total number of attacks and tree diameters. Inclusion of tree resistance into the model had little or no effect on the predictions, due to a rapid attack rate at population levels during this study.

Geiszler and others concluded from their model that, if the total attacks on a tree are limited by a repelling mechanism at high population densities, and the number of repelled beetles is large, these repelled beetles "switch" from the focus tree to attack adjacent trees in overwhelming numbers. They also considered switching attacks a critical factor contributing to outbreaks. Further, if switching can be disrupted (for instance, by thinning stands), the repelled beetles will disperse, numbers will be reduced, and fewer attacks will occur in a new area. Most previous studies have been concerned with host attraction, physiological responses, stand factors, climate, age, and other factors. This study was one of the few (if not the only study) to consider population density of the flying beetles. Failing to include population density in these other studies, particularly the tree susceptibility/resistance studies, may be the reason so many inconsistencies resulted. The results from this modeling of aggregation clearly indicate that population density is important to colonization of the tree, the number of beetles repelled, and subsequent switching from the focus tree. The results were verified, correspondingly, to field observations.

Stand-Beetle Models

Interactions of the beetle with the infested trees, and tree losses to the beetles within stands, follow a predictable pattern. The green stand in which a beetle epidemic might be expected—trees 4 inches (10.2 cm) d.b.h. and larger—contains a relatively large proportion of trees over 12 inches (30.5 cm) in diameter (22 percent in the case described here, fig. 5). A large proportion of trees 12 inches d.b.h. and larger provides the threshold food supply necessary for an epidemic because of the thick phloem found in such trees (Cole and Cahill 1976). The epidemic potential exists primarily under optimal temperatures for beetle development (Amman and Baker 1972; Amman 1973; Safranyik and others 1974).

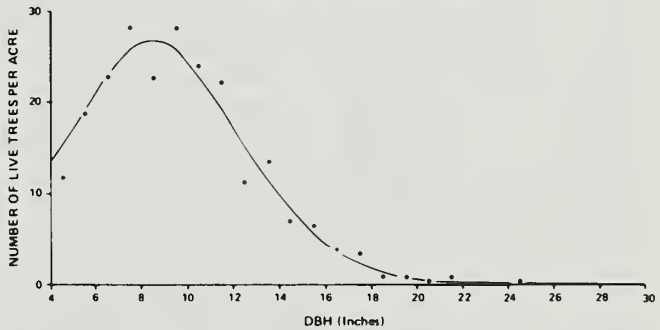


Figure 5.—Green stand structure of lodgepole pine at the beginning of the mountain pine beetle infestation (Cole and others 1976).

Losses of lodgepole pine over the main epidemic years are proportionately much greater in the large diameter classes (fig. 6A). Most tree losses occurred during a 6-year period. Cumulative losses show that most large diameter trees were killed during the infestation (fig. 6B). Losses ranged from about 84 percent of the large trees to about 40 percent of the small trees. Losses shown are typical for stands of trees of similar size and distribution at similar elevations and latitudes in northwestern Wyoming and southeastern Idaho (Amman and Baker 1972).

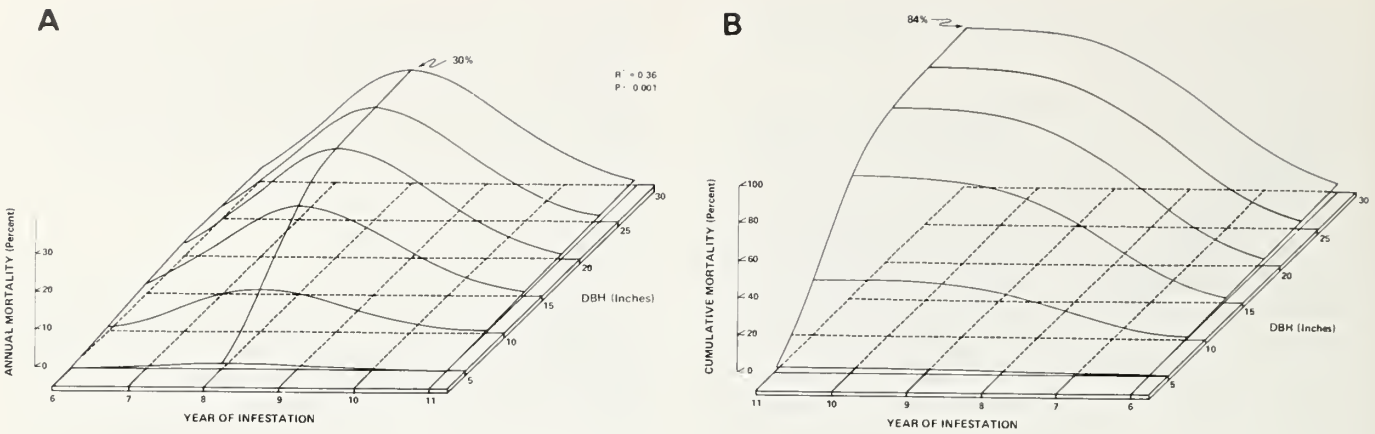


Figure 6.—Losses of lodgepole pine by diameter class and year during an infestation of the mountain pine beetle. A. Annual mortality percent of original stand (r^2 = 0.36; P<0.001); B. cumulative mortality percent.

Stand-beetle interaction models.—Stand models and beetle models were incorporated for selected years spanning the infestation to show interactions. When comparing the green stand and tree mortality models with the beetle brood models for the main epidemic years, the following years essentially correspond: residual stand or annual mortality model year 1 = beetle model years 1 through 5; 2 = 6; 3 = 7; 4 = 8 (peak year); 5 = 9; 6 = 10; and 7 = 11 through 13. Figure 7A represents a year when the beetle population was endemic. Curves by beetle stages show expected survival in a tree of any specific diameter, if it becomes infested.

During year 8, both emergence and tree losses peaked (fig. 7B). Compared to year 1, both egg density and adult emergence approximately doubled. The fact that gallery inches and egg densities continue to rise in following years, but emergence declines, indicates that gallery density and subsequent larval population reached an optimum in year 8. Cumulative tree mortality is substantial, with about half the trees killed by year 8. Numerically, losses appear similar for the different diameter classes. Proportionately, however, losses are much greater for the large diameter classes.

Year 10 (fig. 7C) shows a large increase in eggs, but the number of small larvae surviving through the winter was about the same as in year 8, and the number of surviving large larvae was much reduced. Emergence now approximates the level that occurred during the endemic period (fig. 7A), but tree losses do not. Cumulative tree losses (50 percent) in year 8 have increased to 83 percent by year 10 (fig. 7C), primarily because of high emergence and correspondingly high tree losses during year 9.

In year 12 (fig. 7D), the high egg densities resulted in high larval mortality, probably from severe competition for food and drying of phloem. Subsequent emergence, in accordance with expectations, was even lower than in preepidemic years (1 through 5). Emergence should return to these levels when egg gallery densities return to their original endemic levels (year 1). By year 12, cumulative tree mortality had leveled off and annual tree mortality had returned to the endemic level. Cumulative losses in the stand do not appear overwhelming (fig. 7D). However, most of the trees that were over 12 inches (30.5 cm) d.b.h. had been killed. Mortality ranged from 42 percent of the 12-inch trees to 84 percent for trees 30 inches (76.2 cm) and over.

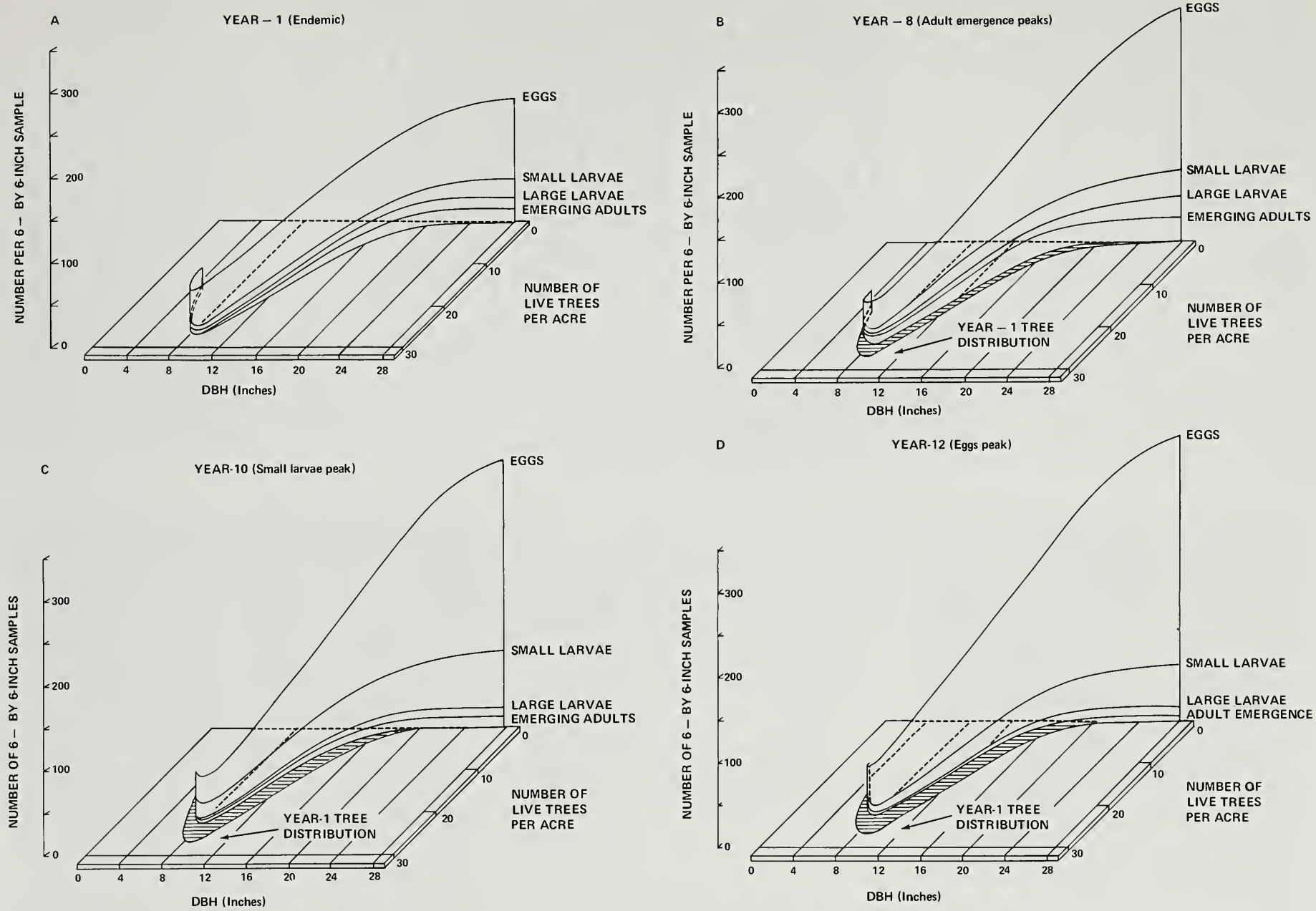


Figure 7.—Interaction models of beetle survival and lodgepole pine losses. A. Year 1 (endemic beetle population level); B. year 8 (peak adult emergence); C. year 10 (peak small larval density); D. year 12 (peak egg density) (Cole and others 1976).

In the interaction models (Cole and others 1976), the close association of beetle dynamics with numbers and sizes of trees that are infested can be seen at any point in the epidemic. For example, emergence diminishes rapidly as the large trees are killed. Beetles then tend to infest a higher proportion of smaller trees. Coincident with this are increased numbers of gallery starts, gallery inches, and subsequent egg densities. These continue to rise through year 12, even though emergence has declined drastically. Brood in small trees having thin phloem tend on the average to have higher proportions of females than are found in large trees having thick phloem (fig. 8), because females survive better under stress than males. W. E. Cole (1973) demonstrated that females survived in greater proportion than males when crowding of larvae increased, and Amman and Rasmussen (1974) found that female survival was greater than that of males when drying of bark increased.

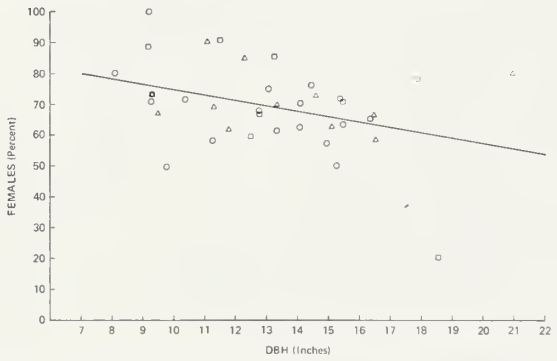


Figure 8.—Proportion of female mountain pine beetles per tree in the emerging population from infested lodgepole pine on the Wasatch National Forest, 1972 to 1974. $\hat{Y} = 91.8 - 1.68x$; $s_{y \cdot x} = 13.1$; $r^2 = 0.13$; $P < 0.025$ (Cole and others 1976).

The increase in density of gallery starts and subsequent gallery inches may be related to a changing sex ratio in the beetle population (fig. 9) (Amman and Cole 1983), as related to the beetles' aggregative and antiaggregative pheromone system. Starting about the time of peak emergence (year 8), it appears that insufficient males exist to mate most females in a relatively short time. Hence, unmated females continue to produce the aggregative pheromone, trans-verbenol, which attracts additional females. Male and mated female mountain pine beetles produce an antiaggregative pheromone that stops additional attacks on the tree (Rudinsky and others 1974).

A synoptic model showing the overall beetle-stand dynamics is presented in figure 10. Survival of females is greater than males within small diameter trees that are infested during early stages of stand development. Attack densities of beetles are high at this time, although limited to the base of the tree, and are related to the low proportion of males in the population. Males, either upon reaching a tree under attack or upon mating, along with mated females, release a chemical messenger (pheromone) that signals arriving females that the tree is occupied,

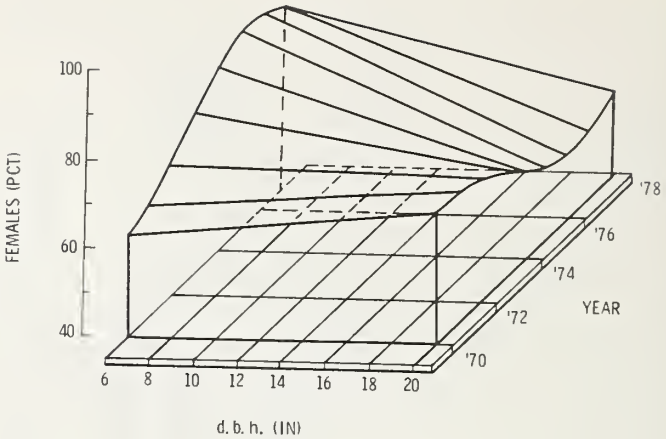


Figure 9.—Sex ratios of mountain pine beetle populations differ by diameter of lodgepole pine and year of infestation, Wasatch-Cache National Forest, UT.

thus countering the aggregative pheromone of the unmated female beetle (Rudinsky 1968). With few males present, the buildup of the antiaggregative pheromone is slow. This results in a high attack density, thereby limiting brood production to some extent. However, on the positive side for such a behavioral mechanism is that sufficient population is usually attracted to kill a tree, thus assuring some brood production.

As the stand grows into pole sizes, with some trees exceeding 16 inches (41 cm) d.b.h., more food in the form of phloem is available; and the sapwood of the large trees is thick so that excessive drying does not occur during beetle brood production. Beetle production is usually low in the widely scattered, small diameter trees infested during the endemic population phase. When several of these infested trees are in close enough proximity that emerging brood key on and infest a common tree of large diameter with thick phloem, brood production is greatly increased. In such trees, production of males and females becomes more even. A more even sex ratio has been associated with reduced attack density because adequate numbers of males are present to rapidly mate all females, resulting in a high concentration of antiaggregative pheromone that stops additional

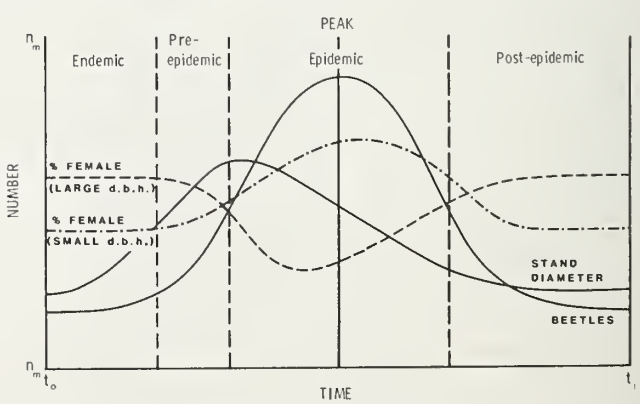


Figure 10.—A synoptic model of the overall mountain pine beetle-lodgepole pine stand dynamics.

female attacks. The result is increased beetle production, followed by a rapid increase in infested trees as the beetle population disperses more efficiently over attacked trees.

When most of the large diameter trees (which usually have thick phloem) are killed, the beetles infest progressively smaller diameter trees (Cole and Amman 1969; Klein and others 1978). Conditions in these trees are similar to those in trees attacked early in the infestation cycle—thin phloem and excessive drying. Brood production is low and sex ratio shifts back toward females in such trees. After the initial infestation in a stand, which may require 60 to 80 years, successive outbreaks can be expected in 20- to 40-year intervals (Roe and Amman 1970). Residual trees are 4 to 10 inches (10.2 to 25.4 cm) d.b.h., with a few trees greater than 10 inches missed by the beetle. Because of the thinning of the stand by the beetles, additional growing space is provided and, within a few years, substantial ingrowth occurs (Klein 1978). Within the 20- to 40-year period, enough large diameter trees with thick phloem are available for another beetle outbreak to occur. In this conceptual model, beetle dynamics are tied to tree and stand dynamics. Stress of trees or stands is not necessary for beetles to become epidemic. As beetle numbers build up, they are able to infest and kill any of the trees.

Tree and stand stress as a factor.—The Cole, Amman, Jensen efforts have avoided tree and stand stress factors as important in the dynamics of mountain pine beetle in lodgepole pine. They use tree diameter as the important element for outbreaks to occur. Larger trees have thick phloem, which is associated with characteristics of good tree vigor (D. M. Cole 1973).

However, Berryman (1976) and Safranyik and others (1975) introduce the element of tree and stand stress as essential for outbreaks to occur. Stress is deemed necessary because large diameter trees with thick phloem are the most vigorous in the stands (D.M. Cole 1973; Shrimpton 1973; Roe and Amman 1970). Stress is considered needed in order for beetles to overcome the trees' resinous defenses. The higher attack densities on large diameter rather than on small diameter trees (Cole and others 1976; Klein and others 1978) are a direct response of the beetles to vigor of these trees. The Berryman (1976) model consists of three variables—phloem thickness, tree resistance, and assumed replacement productivity level for the mountain pine bettle. Stand or tree resistance is measured by periodic growth ratios (PGR),

$$\text{PGR} = \frac{\text{current 5 years radial growth}}{\text{previous 5 years radial growth}}$$

(Mahoney 1978), or a stand hazard rating (SHR), SHR = CCF × %LPPBA (lodgepole pine basal area)(Schenk and others 1980). For a discussion of CCF (crown competition factor) see Krajicek and others (1961). The theoretical model shows that, as phloem thickness increases and stand resistance declines, beetle production increases, thus increasing the chances for a beetle outbreak. Stands that contain less than 10 percent of basal area in trees with phloem ≥0.1 inch (2.5 mm) thick have little or no chance of mountain pine beetle outbreak (Berryman 1978).

Another idea recently introduced as a way to determine susceptibility of trees and stands to mountain pine beetle infestation is growth efficiency (Waring and Pitman 1980). Only those trees with low growth efficiency are believed to be susceptible to successful infestation by mountain pine beetle. The established relation between conifer foliage mass and sapwood area makes growth efficiency relatively easy to measure (Grier and Waring 1974).

A test of SHR and PGR (McGregor 1978; McGregor and others 1981) showed that mortality is inversely, rather than directly, related to SHR, and that mortality is directly related to PGR rather than inversely, as required by the theoretical model (Berryman 1976). McGregor and others (1981), in an examination of 62 lodgepole pine stands in Montana, demonstrated that percentage lodgepole pine mortality increased with reduced CCF (fig. 11). Stands examined were 100 percent

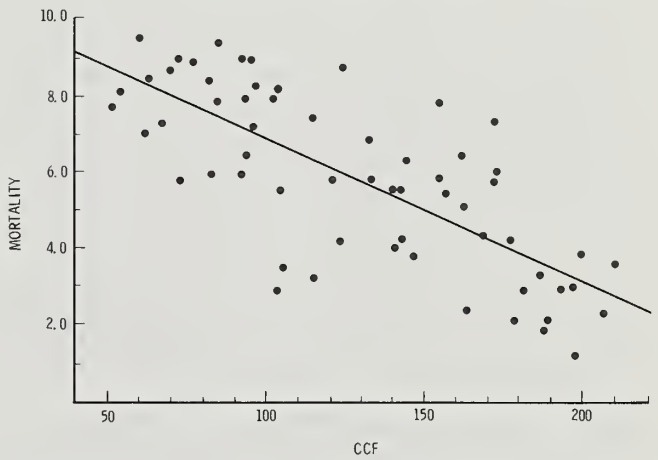


Figure 11.—Losses of lodgepole pine are inversely related to CCF for 62 stands in Montana, 1978 to 1979. Note: Data transformed, $Y' = \sqrt{Y + 3/8}$ *;* $r^2 = 0.57$*;* $P<0.01$.

or nearly 100 percent lodgepole pine; therefore, SHR = CCF. Using the growth efficiency method (Waring and Pitman 1980), four of five stands measured on the Targhee National Forest showed no difference between grams of wood per square meter of foliage for surviving and killed trees ($P > 0.05$) (table 16). A significant difference was shown in the fifth stand ($P < 0.001$); infested trees showed lower growth efficiency than residual green trees. However, dominant and codominant green trees were compared with all trees killed by mountain pine beetle regardless of crown class, in all stands and were much younger. Therefore, the data are biased toward green trees. Using the Berryman model (1978) all five stands were classed low in susceptibility even though three of them had 22 to 30 percent of the lodgepole killed by beetles.

It could be argued that, once populations build up, the relation between the beetle and vigor of the tree changes. Whether a tree can be successfully infested is a function of attack density; that is, the number of available beetles. In other words, when beetles are plentiful, any tree can be infested successfully. At low population

Table 16.—Comparisons of lodgepole pine growth efficiency (Waring – Pitman method) and periodic growth ratios (Mahoney method) between surviving trees and trees killed by mountain pine beetles, Targhee National Forest, ID, 1980

Plot	Grams of wood per m^2 foliage[1]			Periodic growth rate[2]		
	Green trees	Infested trees	t-test	Green trees	Infested trees	t-test
Horseshoe-Packsaddle	56.4	58.9	P > 0.500 NS	0.884	0.873	P > 0.100 NS
Pine Creek	67.0	60.0	P > .400 NS	.939	1.018	P < .001 S
Indian Lake	91.2	75.3	P > .050 NS	1.271	1.303	P > .100 NS
Moody Meadows	76.0	97.4	P > .200 NS	1.067	1.080	P > .500 NS
Warm River	120.9	63.6	P < .001 S	.879	.917	P < .020 S

[1]Susceptibility to beetle infestation:
High = 10-50
Moderate = 51-100
Low = > 100.

[2]Susceptible to attack = < 0.90.
Resistant to attack = > 0.90.

levels difficulty in making a successful attack could be expected. In the Moody Meadows stand on the Targhee National Forest, the fewest infested trees occurred—four infested trees over 4 years = 0.53 tree per acre (1.31/ha) per year. Even at this low infestation rate, PGR's of infested trees ranged between 0.88 and 1.27 ($\bar{x}$ = 1.08). Diameters ranged between 10 and 19 inches d.b.h. (25 to 48 cm), with the 19-inch tree having a PGR of 1.21. Grams of wood per square meter of foliage averaged 97.4 (range 67 to 113). Two of the three trees (sapwood was not measured on the fourth tree) exceeded 100 g/m^2. Trees exceeding that rate have low susceptibility to beetle infestation (G. B. Pitman, letter dated March 25, 1982). If CCF, PGR, and grams of wood per square meter of foliage are indeed good measures of tree and stand vigor, then the relation of mountain pine outbreaks to these variables appears to be reversed. Infestations tend to increase rather than decline with these measures of tree and stand vigor.

Stand growth stress and beetle model.—Stress as a factor in a stand growth-beetle model was introduced by Crookston and others (1978). Stand stress, based on PGR (Mahoney 1978), is used as a mechanism of triggering an epidemic. The mountain pine beetle portion is comprised of two major components. The first is a flight and attack model that includes submodels of emergence, distribution, flight mortality, and effect of beetle-aggregating pheromones. Trees that are attacked and killed are based on the dispersal-aggregation model of Burnell (1977).

This beetle model has been added, as an extension, to the stand growth prognosis model for stand development (Stage 1973). The linkage is presented by Crookston and others (1978). There are three main components:

1. The decision algorithm that controls when the outbreak will occur.
2. The data transmission algorithm that derives required stand parameters.
3. The damage algorithm that reduces the tree population.

The conceptual program flow is shown in figure 12. The probability of an outbreak occurring is based on crown competition factor and the proportion of basal area in lodgepole pine (Schenk and others 1980). However, the relation of CCF and susceptiblity to mountain pine beetle infestation may be valid only for a small part of the lodgepole pine type (Amman in press).

Output of the model is expected stand development from time of inventory until specified rotation. When a beetle epidemic is simulated, information about expected dynamic beetle-tree interactions is generated, including numbers of live and dead trees by d.b.h. class and year of infestation. Algorithms used in these models can be obtained from Crookston and others (1978).

Rate of Tree Loss Model

The rate of loss model refines existing risk-rating systems and provides a method for stratifying lodgepole pine stands and predicting tree and volume loss for habitat types (Cole and McGregor 1983). The model is provided to assist land managers in projecting tree mortality over time, and can be linked to the FORPLAN (Johnson and others 1980) model for use in forest planning.

Most models for epidemic processes have dealt with the continuous-infection model for treating epidemic processes in a fully stochastic manner (that is, probabilistic), and most of these processes dealt with diseases. Consequently, derivatives of the word "infect" rather than "infest" are used. Continuous infection assumes that an individual (the host tree) can be infectious from the moment it receives the infection (the beetle) until it dies, recovers, or is removed. This clearly is not the case with the mountain pine beetle. The mountain pine beetle has a discrete generation and discrete stages of growth, and its epidemic behavior does not fit the continuous-infection assumptions.

An alternative to the continuous-infection assumption was established by Reed and Frost in 1928 (Abbey 1952) and by Greenwood (1931). They postulated that the period of infectiousness is comparatively short, and the latent and incubation periods are constant (Bailey 1957). This alternative assumption best fits the epidemic behavior of the mountain pine beetle and amount of tree

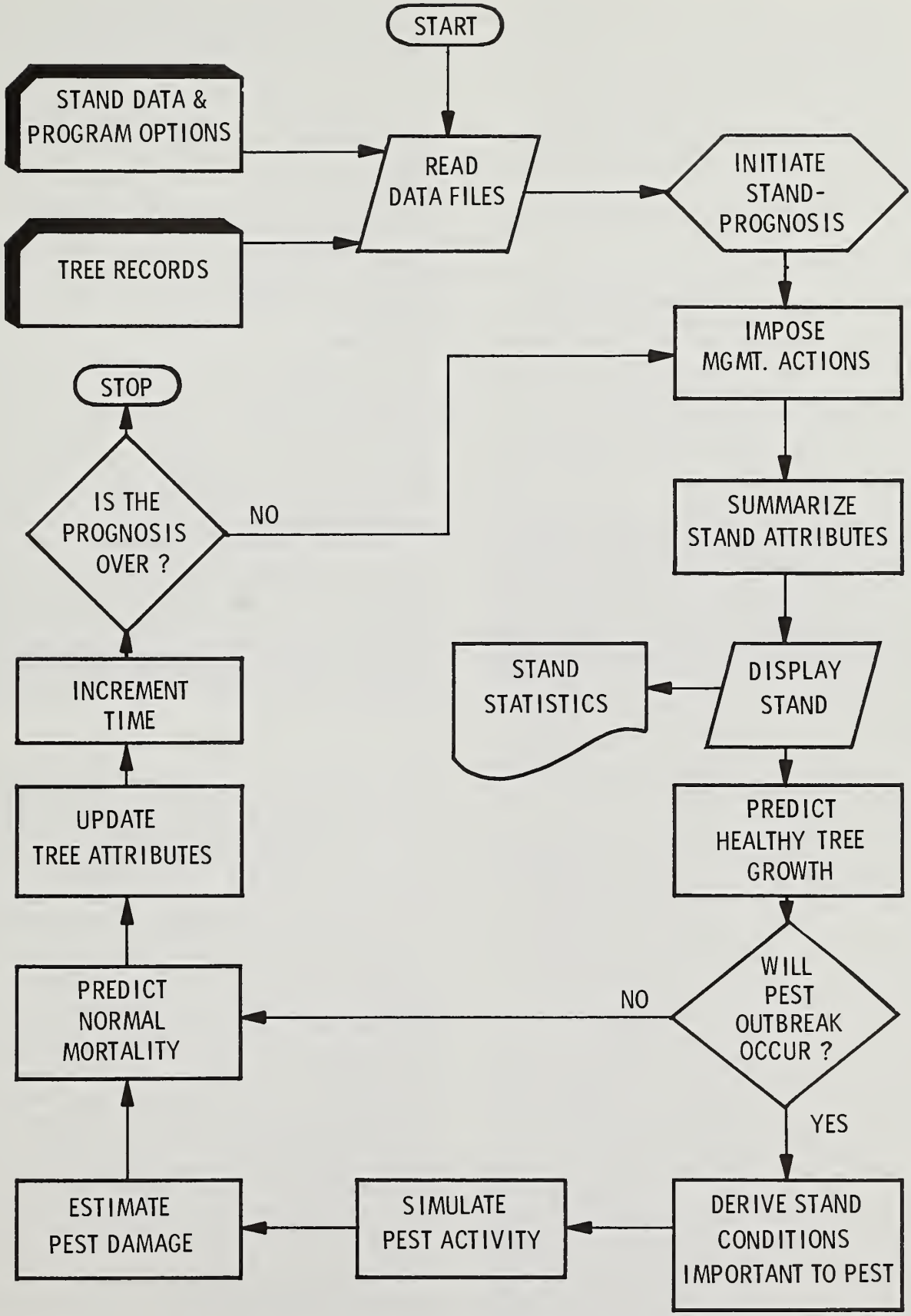


Figure 12.—Conceptual program flow of the stand prognosis model with an optionally linked pest simulation submodel (Crookston 1978).

loss. In lodgepole pine stands in the Intermountain West, the period of infecting a tree (beetle attack) is fairly short (approximately 1 day for one tree and up to 4 to 6 weeks within a stand). The latent period is the time development of the infective that takes place without the emission of any infectious material (brood development). And the incubation period is the elapsed time between the receipt of the infection and the appearance of symptoms (time between attack and foliage discoloration). Both the latent and incubation periods can be considered constant in relation to the life cycle of the beetle and fading of tree foliage.

A first approximation model assumes the following: latent and incubation periods are constant, period of infectiousness is reduced to a single point, and a single attack confers immunity. At each stage in the epidemic, there are certain numbers of infectives and susceptibles, and it is reasonable to suppose that the latter will yield a fresh crop of cases at the next stage, distributed in a binomial series. This results in a chain of binomial distributions, with actual probability of a new infection at any stage being dependent on the numbers of infectives and susceptibles in the previous stage.

Three restrictions of the chain binomial model exist that would invalidate the model: (1) substantial departures from the assumptions of constant incubation and latent periods, (2) a very short infectious period, and (3) failure to properly identify the links of the chain. However, an alternative exists when a highly variable incubation period occurs or the symptoms cannot be identified correctly. In such cases, the analysis can be based on the total number of cases occurring during the course of the epidemic. However, some loss of precision results with estimations. When numbers infected are large, frequencies of infection can be calculated directly and will probably be more accurate than those derived from the probabilities of the individual chains.

Concerning the assumptions of short infectiousness and constant incubation and latent periods, a beetle outbreak can begin with one or several simultaneously infested trees within a stand. The infestation then will spread in a series of stages by each new generation of adult beetles attacking living green trees. If the stand of trees is suitable for successful brood production by the beetles, we expect the number of trees killed at any stage to have a binomial distribution based upon numbers of susceptible and infested trees. Therefore, we have a chain of binomial distributions throughout the course of a mountain pine beetle epidemic. The probability of a tree becoming infested at any generation depends upon the numbers of infested trees and susceptible green trees during the preceding generation of beetles.

Therefore, an epidemic started by beetles from a single infested tree, or by several trees infested simultaneously, will continue in a series of stages (generations of beetles) until either no more beetles are left to attack green trees or no more green trees are left to be attacked. There will be a certain number of infested trees and a certain number of susceptibles in each stage (each beetle generation) of an epidemic. These remaining susceptibles can be attacked by a new generation of beetles, and the newly infested trees will be distributed in a binomial series. Thus, a chain of binomial distributions occurs. The assumptions underlying models based on discrete time usually consider all susceptible and infested individuals to be mixed homogeneously. This situation, more nearly represented by small groups of trees, does not hold with large stands. However, incubation (time interval between the infesting of a tree or stand and the appearance of symptoms) and latent periods (interval in which insect development takes place within the tree) are not variable. Therefore, infesting of a tree is considered a relatively short period. As this model was refined, factors were included that govern tree and stand susceptibility, as well as factors that affect the life processes of beetle population including habitat type, elevation, diameter distribution in a stand, and phloem thickness distribution.

Model description.—If p is the probability of a tree becoming infested in a given time, then $q = 1 - p$ is the probability of a tree not becoming infested. The probability of a tree becoming infested, in this sense, depends on the susceptibility or resistance of the tree, the infestivity of the beetle, the length of attack period, and the size of the attacking beetle population, as well as the environmental conditions of the stand.

If D_t is the number of trees infested at time t, then q^{D_t} is the probability that the specified tree will not be infested, and $1 - q^{D_t}$ is the probability that the tree will be infested. It follows that if there are G_t green trees capable of being infested in the population at time t, the expected number of infested trees produced at the time $t+1$ is G_t times the probability of at least one tree being infested. Or,

$$D_{t+1} = G_t (1 - q^{D_t}) \text{ and } G_{t+1} = G_t q^{D_t}$$

This equation provides a method of stepwise calculation of trees infested at successive periods. Calculations for a theoretical beetle epidemic are presented in table 17. If $G_t = 0$, all the trees are dead and the epidemic subsides due to food depletion. If $D_t = 0$, beetles are no longer reproducing successfully and the epidemic subsides.

The Greenwood model postulates that the probability of a susceptible tree being infested is a constant and is not related to the number of infectives. In other words, a susceptible tree in a stand with one infective is as likely to get attacked as the same tree surrounded by many infectives. This is obviously not the case, because trees adjacent to a freshly attacked tree are more likely to be infested than more distant trees (Geiszler and others 1980). Thus, we adopted the Reed-Frost model for susceptibility because it accounts for the increase in infestation pressure due to the number of infested trees. In the Reed-Frost model, the probability of a tree not being infested from only one source is taken to be a constant, q. The probability of not being infested from two sources is thus (q)(q) and, consequently, from n sources it is q^n.

The value of q can be calculated from these relationships by solving the equation of G_{t+1} for q. This yields

$$q = (G_{t+1} / G_t)^{(1/D_t)}$$

Table 17.—Calculation of theoretical epidemic of mountain pine beetles from the Reed–Frost model (p = 0.5)

Time period	Number of dead trees (D)	Number of susceptible trees (G)	Calculation of D_{t+1} and G_{t+1}
0	1	100	$D_1 = 100 (1 - 0.95) = 5.00 = 5$
			$G_1 = 100 - 5 = 95$
1	5	95	$D_2 = 95 (1 - 0.95^5) = 21.49 = 21$
			$G_2 = 95 - 21 = 74$
2	21	74	$D_3 = 74 (1 - 0.95^{21}) = 48.80 = 29$
			$G_3 = 74 - 49 = 25$
3	49	25	$D_4 = 25 (1 - 0.95^{49}) = 22.97 = 23$
			$G_4 = 25 - 23 = 2$
4	23	2	$D_5 = 2 (1 - 0.95^{23}) = 1.39 = 1$
			$G_5 = 2 - 1 = 1$
5	1	1	$D_6 = 1 (1 - 0.95^7) = 0.05 = 0$
			$G_6 = 1 - 0 = 1$
6	0	1	

Theoretically, q will be a constant, but the real world is never constant. Thus, the q for time (q_t) varies slightly with t and may be determined for each time interval. However, a closer prediction of D_{t+1} can be obtained when several values for q_t are calculated, and q estimated by q_t for several stands.

Testing the model.—Two sets of published data were used to test the model. The first set came from a mountain pine beetle infestation in the Bechler River Drainage of Yellowstone National Park (Klein and others 1978). These data were grouped into the following categories: (1) by 2-inch (5.1-cm) diameter classes; (2) by 6- to 12-inch (15.2- to 30.5-cm), 14- to 16-inch (35.6- to 40.6-cm), and greater than 16-inch (40.6-cm) d.b.h. classes; and (3) by total stand (tables 18 and 19) (figs. 13 and 14). From these, tree losses were predicted for this stand. A close fit to actual losses was obtained.

Table 18.—Predicted versus observed tree losses to the mountain pine beetle by year based on $\bar{q}_t$, for 2-inch (5.1-cm) tree diameter classes (Situation A, observed data from Klein and others 1978)

Diameter class	Year of infestation	Number of trees per acre: Green (G)	Number of trees per acre: Dead (D)	$1/D_t$	q_t[1]	Predicted tree loss
6-inch	0	79.8	0.3	3.333	0.9875	0.14
(15.2-cm)	1	79.5	0	0	1.0000	0
	2	79.5	.3	3.333	.9857	.14
	3	79.2	2.1	.476	.9873	.99
	4	77.1	0	0	1.0000	0
	5	77.1	0	0	1.0000	0
	6	77.1	0	0		0
		Total loss	2.7	Average	0.9937	1.27
			(1.1/ha)			(0.51/ha)
8-inch	0	62.7	0.8	1.250	0.984	0.90
(20.3-cm)	1	61.9	.8	1.250	.984	.89
	2	61.1	2.7	.370	.983	2.92
	3	58.4	8.1	.120	.982	7.99
	4	50.3	.7	1.430	.980	.63
	5	49.6	.5	2.000	.980	.63
	6	49.1	0	0		0
		Total loss	13.6	Average	0.982	13.96
			(3.4/ha)			(5.6/ha)
10-inch	0	38.8	0.8	1.250	0.974	1.09
(25.4-cm)	1	38.0	1.1	.909	.974	1.46
	2	36.9	3.9	.256	.972	4.79
	3	33.0	10.6	.094	.964	10.38
	4	22.4	1.4	.714	.955	1.09
	5	21.0	.6	1.667	.953	.44
	6	20.4	.2	5.000		.14
	7	20.2	0	0		0
		Total loss	18.6	Average	0.965	19.39
			(7.4/ha)			(7.8/ha)
12-inch	0	17.0	0.6	1.667	0.942	0.95
(30.5-cm)	1	16.4	1.3	.769	.938	1.91
	2	15.1	2.8	.357	.932	3.54
	3	12.3	4.2	.238	.902	4.06
	4	8.1	1.2	.833	.875	.88
	5	6.9	.2	5.000	.863	.13
	6	6.7	.1	10.000		.64
	7	6.6	0	0		0
		Total loss	10.4	Average	0.909	11.87
			(4.2/ha)			(4.7/ha)
14-inch	0	8.0	0.4	2.500	0.880	0.89
(35.6-cm)	1	7.6	1.2	.833	.867	2.28
	2	6.4	2.2	.454	.826	3.07
	3	4.2	2.0	.500	.724	1.88
	4	2.2	.4	2.500	.606	.25
	5	1.8	.2	5.000	.55	.10
	6	1.6	0	0		0
		Total loss	6.4	Average	0.743	8.47
			(2.6/ha)			(3.4/ha)
16-inch	0	2.1	0.3	3.333	0.598	0.624
(40.6-cm)	1	1.8	.3	3.333	5.45	.534
	2	1.5	.7	1.429	.407	.841
	3	.8	.3	3.333	.209	.238
	4	.5	.2	5.000	.078	.105
	5	.3	.1	10.000	.017	.033
	6	.2	0	0		0
		Total loss	1.9	Average	.309	2.375
			(0.8/ha)			(0.9/ha)

(con.)

Table 18. (Con.)

Diameter class	Year of infestation	Number of trees per acre: Green (G)	Number of trees per acre: Dead (D)	$1/D_t$	q_t[1]	Predicted tree loss
>16-inch	0	2.0	0.3	3.333	0.582	0.63
(>40.6-cm)	1	1.7	.4	2.500	.511	.67
	2	1.3	.9	1.111	.270	.88
	3	.4	.1	10.000	.056	.05
	4	.3	.2	5.000	.004	.06
	5	.1	0	0	0	0
	6	.1	0			0
		Total loss	1.9 (0.8/ha)	Average	0.285	2.29 (0.9/ha)
Total	0	211.0	3.0			5.2
	1	208.0	5.0			7.7
	2	203.0	14.0			16.2
	3	189.0	27.0			15.6
	4	162.0	4.0			3.0
	5	158.0	2.0			1.3
	6	156.0	1.0			.2
	7	155.0	0			0
		Total loss	56.0 (22.5/ha)	Average	0.753	59.2 (28.3/ha)

[1] q_t is the probability of a tree not being infested from one source during time, t.

Table 19.—Predicted versus observed tree losses to mountain pine beetles by year based on $\bar{q}_t$, the average probability of tree loss by tree diameter class and stand (Situation A, observed data from Klein and others 1978, grouped by larger diameter classes)

Diameter class	Year of infestation	Number of trees per acre: Green (G)	Number of trees per acre: Dead (D)	$1/D_t$	q_t	Predicted tree loss
6–12-inch	0	198.3	2.5	0.400	0.997	2.5
(15.2–30.5-cm)	1	196.8	3.2	.313	.995	3.1
	2	193.6	9.7	.103	.995	9.2
	3	183.9	25.0	.040	.994	21.7
	4	158.9	3.3	.303	.994	2.6
	5	155.6	1.3	.769	.994	1.0
	6	154.3	.3	3.333	0	.2
	7	154.0	0	0		
		Total loss	44.3 (17.7/ha)	Average	0.995	40.3 (16.1/ha)
14–16-inch	0	12.1	1.0	1.000	0.917	2.5
(35.6–40.6-cm)	1	11.1	1.9	.526	.906	3.9
	2	9.2	3.8	.263	.869	5.4
	3	5.4	2.4	.416	.783	2.3
	4	3.0	.8	1.250	.679	.5
	5	2.2	.3	3.333	.613	.15
	6	1.9	0	0	0	0
		Total loss	10.2 (4.1/ha)	Average	0.794	14.8 (5.9/ha)
> 16-inch	0	4.1	0.6	1.667	0.768	1.6
(> 40.6-cm)	1	3.5	.7	1.429	.727	1.7
	2	2.8	1.6	.625	.589	2.0
	3	1.2	.4	2.500	.363	.3
	4	.8	.4	2.500	.177	.2
	5	.4	.4	10.000	.056	.03
	6	.3	0	0	0	0
		Total loss	3.8 (1.5/ha)	Average	0.447	5.9 (2.4/ha)

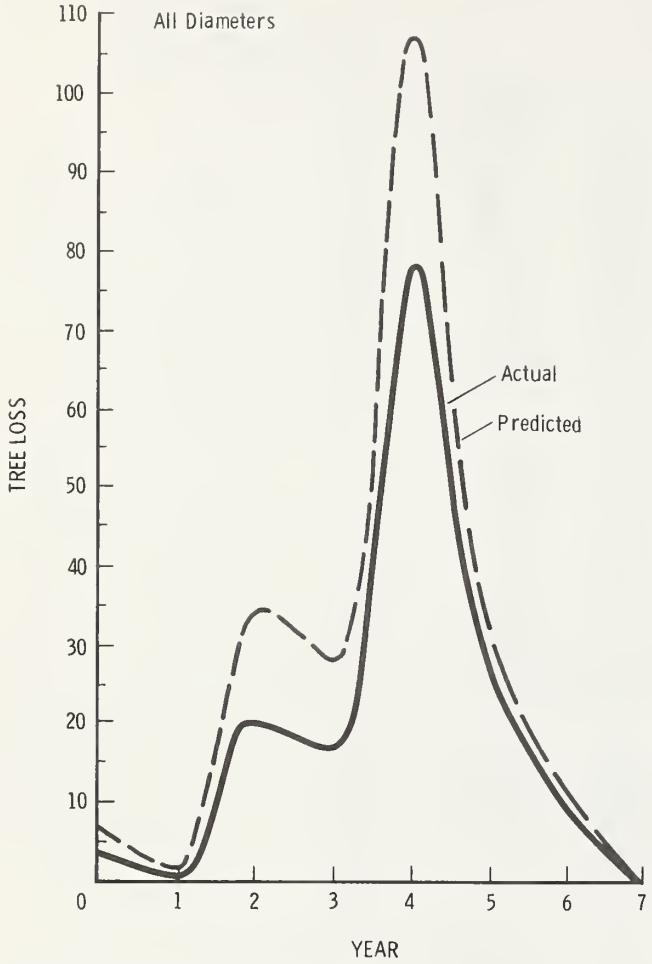


Figure 13.—Predicted versus observed tree losses to mountain pine beetles by year, based on $\bar{q}_t$, by tree diameter class, grouped and total stand (observed losses from Burnell 1977). q_t is the probability of a tree not being infested from one source during time, t.

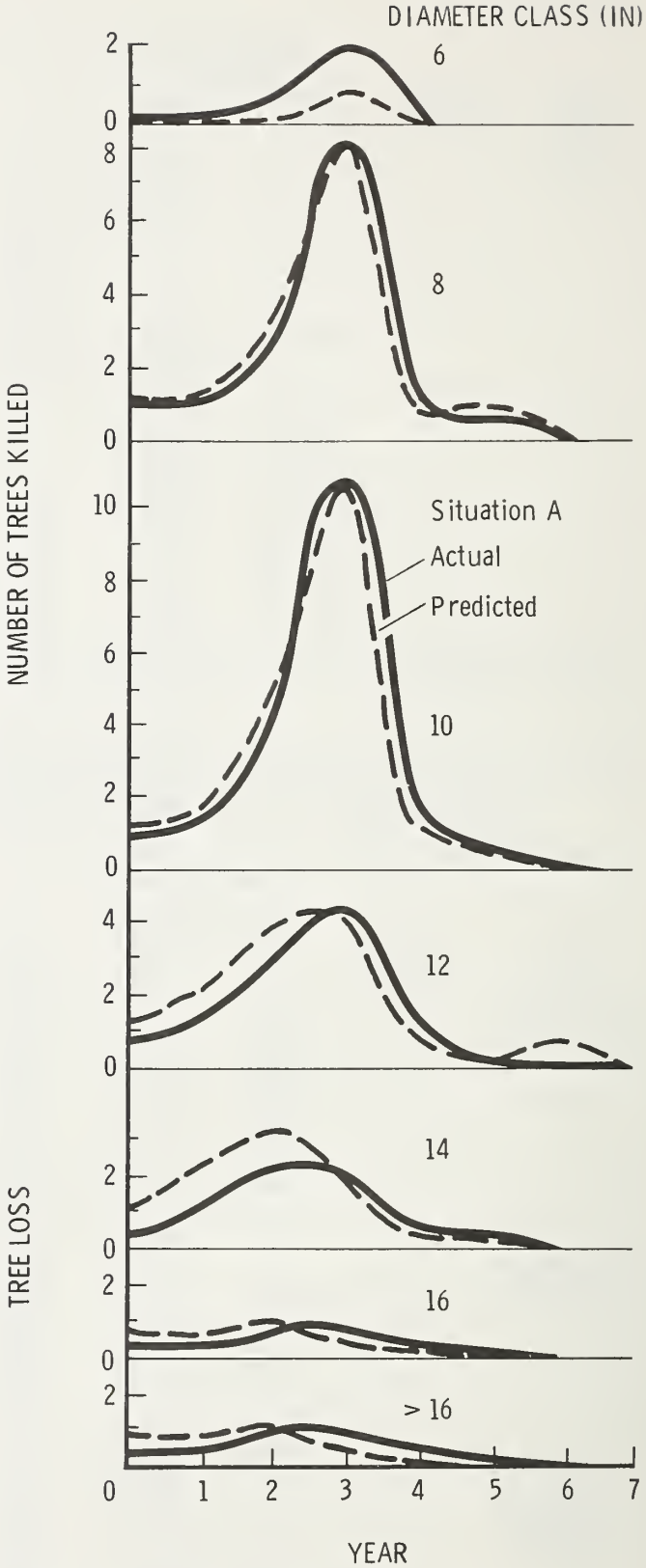


Figure 14.—Predicted versus observed tree losses to mountain pine beetles in lodgepole pine by year, based on $\bar{q}_t$, by 2-inch tree diameter classes (observed losses from Klein and others 1978).

Table 20.—Predicted versus observed tree losses to mountain pine beetles by year based on $\bar{q}_t$, the average probability of tree loss by tree diameter class and stand (Situation B, observed data from Burnell 1977, grouped by total stand)

Year of infestation	Number of trees per acre: Green (G)	Number of trees per acre: Dead (D)	$1/D_t$	q_t	Predicted tree loss
0	370.2	3.6	0.278	0.997	6.6
1	366.6	.8	1.250	.997	1.5
2	365.8	19.5	.051	.997	34.1
3	346.3	16.4	.061	.997	27.3
4	329.9	77.8	.013	.999	106.5
5	252.1	31.8	.032	.992	37.1
6	220.3	10.3	.097	.987	11.1
7	210.0	0	0	0	0
	Total loss	160.2 (64.1/ha)	Average	0.995	224.2 (89.7/ha)

The second data set came from a mountain pine beetle infestation in the Gallatin River Drainage (Burnell 1977) and was used only for total tree loss because the data were not presented by diameter classes. In this data set, tree loss over time did not fall into the usual bell-shaped pattern. However, predicted tree losses approximated the double-peaked curve (table 20) (fig. 15).

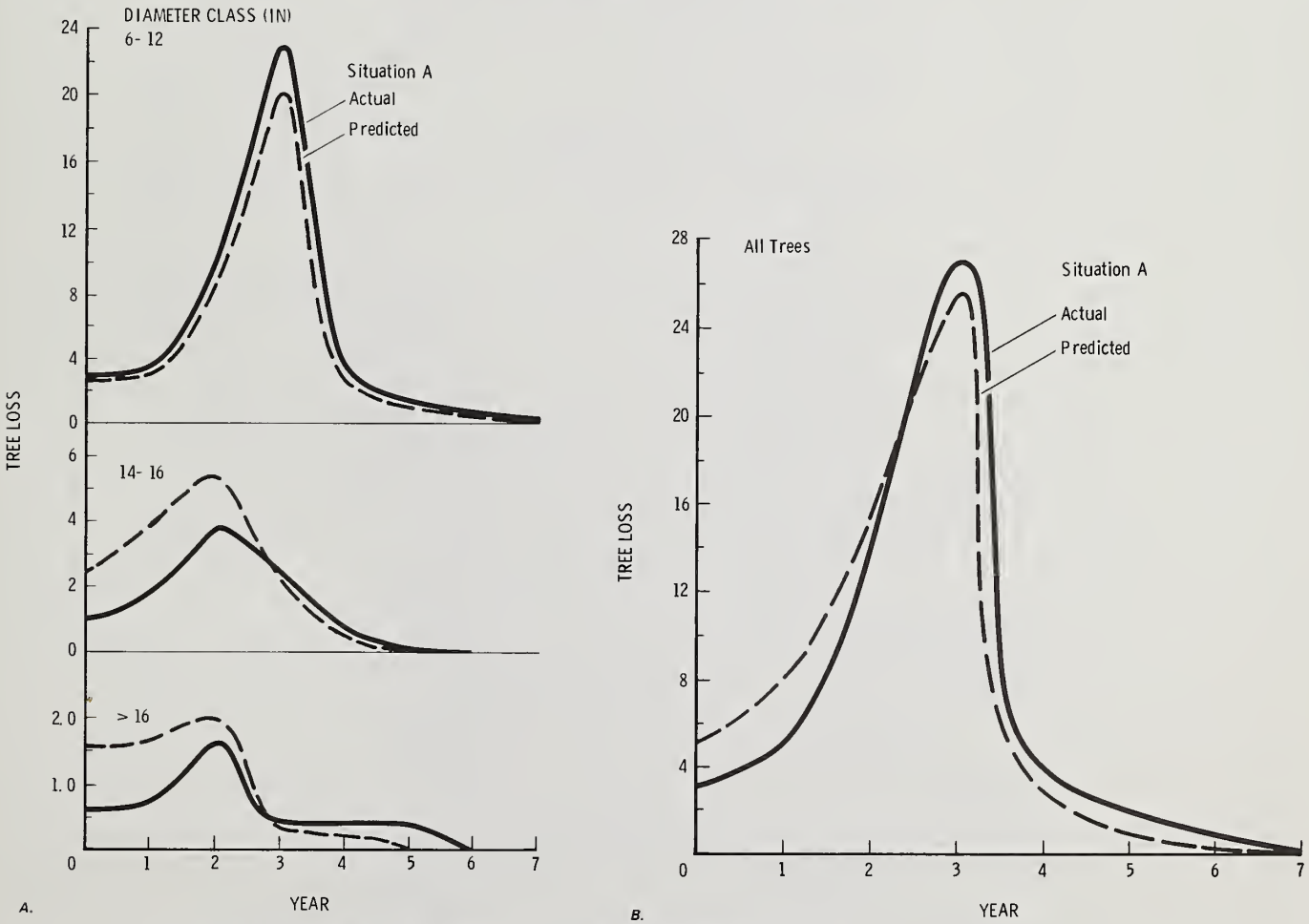


Figure 15.—Predicted versus observed tree losses to mountain pine beetles in lodgepole pine by year, based on $\bar{q}_t$. A. Grouped by tree diameter classes; B. for total stand (observed losses from Klein and others 1978).

Precision of prediction increases with decreasing size of diameter classes; that is, estimates of tree mortality over time approximate true losses closer when predicted by 2-inch (5.1-cm) diameter classes than by larger diameter classes (figs. 13 and 14).

Peak mortality tended to be overestimated when q was large. By the third year of an infestation, q usually becomes small due to the loss of large diameter trees to beetles. Consequently, tree mortality is overestimated. The critical time during an infestation by the mountain pine beetle is at the point of change from endemic to epidemic. The value q applied to the larger diameter trees forecasts the pending infestation adequately, in spite of the tendency toward overestimation.

The model assumes optimum conditions for the life of the epidemic. However, actual field conditions (for example, adverse weather) can cause beetle populations to deviate from predictions. Overestimation of tree mortality is not considered serious in most cases, particularly in the larger diameter classes. Epidemics usually begin in larger diameter trees preferred by the mountain pine beetle, and the rate of tree loss within these classes is critical. Thus, any factor that affects brood survival, such as thick phloem (food supply), which is correlated with larger diameters, will affect the rate of tree loss and, in turn, successive generations.

Linking to INDIDS model.—The INDIDS model (Bousfield 1981) is used to analyze forest insect and disease data collected from variable or fixed plots. It provides summaries of detailed mensurational data of infested and residual green stands, a tree species, size class, and damage class for each designated survey type. The INDIDS model also computes tree and volume losses and basal area killed per acre.

The rate of loss and INDIDS models were linked to estimate mortality trends for stands with ongoing mortality or to obtain loss estimates (tree, cubic, and board-foot volumes) by diameter class over infestation time for green stands, should they become infested (table 21). The INDIDS/rate of loss model was tested, using approximately 1,200 stands with varying degrees of mountain pine beetle infestation (ranging from 1 year to the end of the epidemic) (McGregor and others 1982).

Table 21.—Estimated trees per acre and volume losses by diameter class over time, using the rate of loss model for mountain pine beetle in lodgepole pine

a. Mixed species stand: 25.4 percent subalpine fir, 12.4 percent Engelmann spruce, 12.4 percent whitebark pine, 37.3 percent lodgepole pine, 12.4 percent Douglas-fir

Item	Diameter at breast height										
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total
Lodgepole Pine Trees and Cubic Foot Volume per Acre Before an Outbreak											
Live trees	.00	.00	.00	.00	.00	31.85	31.37	.00	9.32	.00	72.54
Dead trees	.00	.00	.00	.00	.00	1.12	1.57	.00	1.40	.00	4.09
Cubic feet	.00	.00	.00	.00	.00	691.56	943.91	.00	457.15	.00	2,092.62

Trees per Acre Killed During 10-Year Outbreak

	Diameter at breast height																			
	0-2.9		3-4.9		5-6.9		7-8.9		9-10.9		11-12.9		13-14.9		15-16.9		17-18.9		19+	
Year	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
1	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	27.6	3.12	18.7	11.10	.0	.00	1.4	6.55	.0	.00
2	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	20.5	7.12	.7	18.01	.0	.00	.0	1.37	.0	.00
3	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	10.4	10.09	.0	.69	.0	.00	.0	.00	.0	.00
4	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	4.0	6.42	.0	.00	.0	.00	.0	.00	.0	.00
5	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	2.1	1.82	.0	.00	.0	.00	.0	.00	.0	.00
6	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	1.8	.34	.0	.00	.0	.00	.0	.00	.0	.00
7	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	1.7	.06	.0	.00	.0	.00	.0	.00	.0	.00
8	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	1.7	.01	.0	.00	.0	.00	.0	.00	.0	.00
9	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	1.7	.00	.0	.00	.0	.00	.0	.00	.0	.00
10	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00	1.7	.00	.0	.00	.0	.00	.0	.00	.0	.00

Lodgepole Pine Trees and Cubic Foot Volume per Acre After an Outbreak

	Diameter at breast height											Percent mortality
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total	
T/A	.00	.00	.00	.00	.00	1.74	.00	.00	.00	.00	1.74	97.6
CFA	.00	.00	.00	.00	.00	37.72	.08	.00	.00	.00	37.80	98.2

Attack	Unsec	LP Total	Percent
.00	.00	56.54	.00
Attack CFA	Unsec CFA	LPCFV Total	Percent CFV
.00	.00	1,608.99	.00

(con.)

Table 21. (Con.)
b. Mixed species stand: 15 percent lodgepole pine, 85 percent Douglas-fir, subalpine fir, Engelmann spruce

Item	Diameter at breast height										
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total
Lodgepole Pine Trees and Cubic Foot Volume per Acre Before an Outbreak											
Live trees	.00	.00	.00	.00	6.91	.00	11.46	.00	.00	.00	18.38
Dead trees	.00	.00	.00	.00	.14	.00	.57	.00	.00	.00	.72
Cubic feet	.00	.00	.00	.00	143.42	.00	323.26	.00	.00	.00	466.68

Trees per Acre Killed During 10-Year Outbreak

	Diameter at breast height																			
	0-2.9		3-4.9		5-6.9		7-8.9		9-10.9		11-12.9		13-14.9		15-16.9		17-18.9		19+	
Year	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
1	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.03	.0	.00	9.2	1.70	.0	.00	.0	.00	.0	.00
2	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.01	.0	.00	5.5	3.65	.0	.00	.0	.00	.0	.00
3	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	1.9	3.66	.0	.00	.0	.00	.0	.00
4	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	.6	1.24	.0	.00	.0	.00	.0	.00
5	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	.4	.19	.0	.00	.0	.00	.0	.00
6	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	.4	.02	.0	.00	.0	.00	.0	.00
7	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	.4	.00	.0	.00	.0	.00	.0	.00
8	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	.4	.00	.0	.00	.0	.00	.0	.00
9	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	.4	.00	.0	.00	.0	.00	.0	.00
10	.0	.00	.0	.00	.0	.00	.0	.00	6.7	.00	.0	.00	.4	.00	.0	.00	.0	.00	.0	.00

Lodgepole Pine Trees and Cubic Foot Volume per Acre After an Outbreak

	Diameter at breast height											Percent mortality
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total	
T/A	.00	.00	.00	.00	6.73	.00	.41	.00	.00	.00	7.13	61.2
CFA	.00	.00	.00	.00	139.53	.00	11.51	.00	.00	.00	151.04	67.6

Attack	Unsec	LP Total	Percent
.00	.00	10.45	.00
Attack CFA	**Unsec CFA**	**LPCFV Total**	**Percent CFV**
.00	.00	242.77	.00

(con.)

Table 21. (Con.)
c. Mixed species stand: 65 percent subalpine fir, 29 percent Engelmann spruce, 6 percent lodgepole pine

Item	Diameter at breast height										
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total
Lodgepole Pine Trees and Cubic Foot Volume per Acre Before an Outbreak											
Live trees	.00	60.00	33.67	176.07	30.58	49.86	14.09	12.30	.00	4.11	380.68
Dead trees	.00	.00	.13	2.25	.63	1.76	.70	1.76	.00	.62	7.85
Cubic feet	.00	.00	149.92	1,452.10	417.93	1,271.31	455.69	495.95	.00	247.44	4,490.34

Trees per Acre Killed During 10-Year Outbreak

	Diameter at breast height																	
	0-2.9		3-4.9		5-6.9		7-8.9		9-10.9		11-12.9		13-14.9		15-16.9		17-18.9		19+	
Year	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
1	.0	.00	60.0	.00	33.5	.03	166.8	6.97	29.3	.66	40.7	7.44	10.9	2.53	1.3	9.20	.0	.00	1.6	1.88
2	.0	.00	60.0	.00	33.5	.01	147.0	19.85	28.6	.69	20.0	20.66	5.1	5.73	.0	1.34	.0	.00	.2	1.46
3	.0	.00	60.0	.00	33.5	.00	102.5	44.49	27.9	.69	2.8	17.22	.9	4.19	.0	.00	.0	.00	.0	.13
4	.0	.00	60.0	.00	33.5	.00	45.7	56.82	27.2	.68	.5	2.25	.3	.66	.0	.00	.0	.00	.0	.00
5	.0	.00	60.0	.00	33.5	.00	16.3	29.41	26.6	.65	.4	.10	.2	.05	.0	.00	.0	.00	.0	.00
6	.0	.00	60.0	.00	33.5	.00	9.5	6.74	26.0	.61	.4	.00	.2	.00	.0	.00	.0	.00	.0	.00
7	.0	.00	60.0	.00	33.5	.00	8.4	1.10	25.4	.56	.4	.00	.2	.00	.0	.00	.0	.00	.0	.00
8	.0	.00	60.0	.00	33.5	.00	8.3	.17	24.9	.50	.4	.00	.2	.00	.0	.00	.0	.00	.0	.00
9	.0	.00	60.0	.00	33.5	.00	8.2	.03	24.5	.44	.4	.00	.2	.00	.0	.00	.0	.00	.0	.00
10	.0	.00	60.0	.00	33.5	.00	8.2	.00	24.1	.38	.4	.00	.2	.00	.0	.00	.0	.00	.0	.00

Lodgepole Pine Trees and Cubic Foot Volume per Acre After an Outbreak

	Diameter at breast height											Percent mortality
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total	
T/A	.00	60.00	33.51	8.25	24.10	.43	.22	.00	.00	.02	126.52	66.8
CFA	.00	.00	149.19	68.01	329.32	10.98	7.02	.00	.00	1.25	565.76	87.4

Attack	Unsec	LP Total	Percent
.00	.00	190.20	.00
Attack CFA	**Unsec CFA**	**LPCFV Total**	**Percent CFV**
.00	.00	2,256.65	.00

(con.)

Table 21. (Con.)
d. Mixed species stand: 10 percent subalpine fir, 77.1 percent lodgepole pine, 12.6 percent Douglas-fir

Item	Diameter at breast height										
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total
Lodgepole Pine Trees and Cubic Foot Volume per Acre Before an Outbreak											
Live trees	94.74	.00	72.32	99.93	48.68	34.83	14.25	3.28	1.14	1.65	370.82
Dead trees	.00	.00	11.47	18.72	11.95	14.48	5.89	.47	1.14	1.65	65.77
Cubic feet	.00	.00	303.49	925.85	775.39	755.39	435.55	137.38	75.42	141.69	3,550.61

Trees per Acre Killed During 10-Year Outbreak

	Diameter at breast height																	
	0-2.9		3-4.9		5-6.9		7-8.9		9-10.9		11-12.9		13-14.9		15-16.9		17-18.9		19+	
Year	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
1	94.7	.00	.0	.00	56.5	4.39	57.8	23.41	24.0	12.73	5.1	15.24	1.5	6.91	1.6	1.19	.0	.00	.0	.00
2	94.7	.00	.0	.00	54.9	1.59	37.8	20.02	15.2	8.75	1.2	3.92	.2	1.27	.4	1.22	.0	.00	.0	.00
3	94.7	.00	.0	.00	54.3	.57	26.3	11.52	11.2	4.09	.8	.37	.1	.06	.1	.31	.0	.00	.0	.00
4	94.7	.00	.0	.00	54.1	.20	21.3	4.96	9.7	1.51	.8	.03	.1	.00	.1	.03	.0	.00	.0	.00
5	94.7	.00	.0	.00	54.0	.07	19.5	1.84	9.1	.51	.8	.00	.1	.00	.1	.00	.0	.00	.0	.00
6	94.7	.00	.0	.00	54.0	.02	18.8	.64	9.0	.16	.8	.00	.1	.00	.1	.00	.0	.00	.0	.00
7	94.7	.00	.0	.00	54.0	.01	18.6	.22	8.9	.05	.8	.00	.1	.00	.1	.00	.0	.00	.0	.00
8	94.7	.00	.0	.00	54.0	.00	18.5	.07	8.9	.02	.8	.00	.1	.00	.1	.00	.0	.00	.0	.00
9	94.7	.00	.0	.00	54.0	.00	18.5	.02	8.9	.01	.8	.00	.1	.00	.1	.00	.0	.00	.0	.00
10	94.7	.00	.0	.00	54.0	.00	18.5	.01	8.9	.00	.8	.00	.1	.00	.1	.00	.0	.00	.0	.00

Lodgepole Pine Trees and Cubic Foot Volume per Acre After an Outbreak

	Diameter at breast height											
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total	Percent mortality
T/A	94.74	.00	53.99	18.51	8.91	.79	.13	.06	.00	.00	177.13	52.2
CFA	.00	.00	226.57	171.48	138.38	17.61	3.85	2.70	.00	.00	560.49	84.2

Attack	Unsec	LP Total	Percent
65.31	.00	161.67	40.39
Attack CFA	**Unsec CFA**	**LPCFV Total**	**Percent CFV**
1,118.04	.00	1,709.80	65.39

(con.)

Table 21. (Con.)
e. Mixed species stand: 28.6 percent subalpine fir, 0.2 percent whitebark pine, 60.6 percent lodgepole pine

Item	Diameter at breast height										
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total
Lodgepole Pine Trees and Cubic Foot Volume per Acre Before an Outbreak											
Live trees	245.45	.00	16.28	8.81	59.05	24.13	3.95	.00	.00	.00	357.66
Dead trees	.00	.00	.06	8.81	26.13	9.93	.20	.00	.00	.00	45.13
Cubic feet	.00	.00	57.19	78.37	840.12	501.31	94.03	.00	.00	.00	1,571.02

Trees per Acre Killed During 10-Year Outbreak

	Diameter at breast height																			
	0-2.9		3-4.9		5-6.9		7-8.9		9-10.9		11-12.9		13-14.9		15-16.9		17-18.9		19+	
Year	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
1	245.5	.00	.0	.00	16.2	.01	.0	.00	13.0	19.94	5.5	8.69	3.5	.21	.0	.00	.0	.00	.0	.00
2	245.5	.00	.0	.00	16.2	.00	.0	.00	6.4	6.60	2.4	3.10	3.3	.22	.0	.00	.0	.00	.0	.00
3	245.5	.00	.0	.00	16.2	.00	.0	.00	5.0	1.34	1.8	.62	3.1	.21	.0	.00	.0	.00	.0	.00
4	245.5	.00	.0	.00	16.2	.00	.0	.00	4.8	.23	1.7	.10	2.9	.19	.0	.00	.0	.00	.0	.00
5	245.5	.00	.0	.00	16.2	.00	.0	.00	4.8	.04	1.7	.02	2.8	.16	.0	.00	.0	.00	.0	.00
6	245.5	.00	.0	.00	16.2	.00	.0	.00	4.8	.01	1.7	.00	2.6	.13	.0	.00	.0	.00	.0	.00
7	245.5	.00	.0	.00	16.2	.00	.0	.00	4.8	.00	1.7	.00	2.5	.10	.0	.00	.0	.00	.0	.00
8	245.5	.00	.0	.00	16.2	.00	.0	.00	4.8	.00	1.7	.00	2.5	.07	.0	.00	.0	.00	.0	.00
9	245.5	.00	.0	.00	16.2	.00	.0	.00	4.8	.00	1.7	.00	2.4	.05	.0	.00	.0	.00	.0	.00
10	245.5	.00	.0	.00	16.2	.00	.0	.00	4.8	.00	1.7	.00	2.4	.04	.0	.00	.0	.00	.0	.00

Lodgepole Pine Trees and Cubic Foot Volume per Acre After an Outbreak

	Diameter at breast height											Percent mortality
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total	
T/A	245.5	.00	16.21	.00	4.76	1.67	2.38	.00	.00	.00	270.47	24.6
CFA	.00	.00	56.94	.00	67.68	34.60	56.78	.00	.00	.00	216.01	86.3

Attack	Unsec	LP Total	Percent
44.87	.00	278.91	16.09
Attack CFA	Unsec CFA	LPCFV Total	Percent CFV
710.12	.00	1,247.91	56.90

(con.)

Table 21. (Con.)
f. Pure lodgepole pine stand

Item	Diameter at breast height										
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total
Lodgepole Pine Trees and Cubic Foot Volume per Acre Before an Outbreak											
Live trees	85.71	300.00	141.46	48.95	22.59	.00	.00	8.35	.00	.00	607.07
Dead trees	.00	.00	.54	.63	.47	.00	.00	1.19	.00	.00	2.82
Cubic feet	.00	.00	484.47	459.73	301.62	.00	.00	258.85	.00	.00	1,504.67

Trees per Acre Killed During 10-Year Outbreak

	Diameter at breast height																			
	0-2.9		3-4.9		5-6.9		7-8.9		9-10.9		11-12.9		13-14.9		15-16.9		17-18.9		19+	
Year	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
1	85.7	.00	300.0	.00	140.4	.49	47.8	.55	21.8	.36	.0	.00	.0	.00	1.8	5.39	.0	.00	.0	.00
2	85.7	.00	300.0	.00	140.0	.45	47.3	.47	21.5	.28	.0	.00	.0	.00	.0	1.76	.0	.00	.0	.00
3	85.7	.00	300.0	.00	139.6	.41	46.9	.40	21.3	.21	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00
4	85.7	.00	300.0	.00	139.2	.37	46.6	.34	21.1	.16	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00
5	85.7	.00	300.0	.00	138.9	.34	46.3	.29	21.0	.12	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00
6	85.7	.00	300.0	.00	138.6	.31	46.0	.24	20.9	.09	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00
7	85.7	.00	300.0	.00	138.3	.28	45.8	.20	20.8	.07	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00
8	85.7	.00	300.0	.00	138.0	.25	45.7	.17	20.8	.05	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00
9	85.7	.00	300.0	.00	137.8	.22	45.5	.14	20.7	.04	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00
10	85.7	.00	300.0	.00	137.6	.20	45.4	.11	20.7	.03	.0	.00	.0	.00	.0	.00	.0	.00	.0	.00

Lodgepole Pine Trees and Cubic Foot Volume per Acre After an Outbreak

	Diameter at breast height											Percent mortality
	0-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19+	Total	
T/A	85.71	300.00	137.60	45.40	20.72	.00	.00	.00	.00	.00	589.43	2.9
CFA	.00	.00	471.24	426.41	276.58	.00	.00	.01	.00	.00	1,174.25	22.0

Attack	Unsec	LP Total	Percent
.00	.00	559.90	.00
Attack CFA	Unsec CFA	LPCFV Total	Percent CFV
.00	.00	1,375.11	.00

Stand data were then subjected to analysis of variance and analysis of covariance for completely randomized design, and graphed to show lodgepole pine mortality by habitat type over time (fig. 16). Analysis shows that the percentage of lodgepole pine killed and volume loss is significantly related to habitat type.

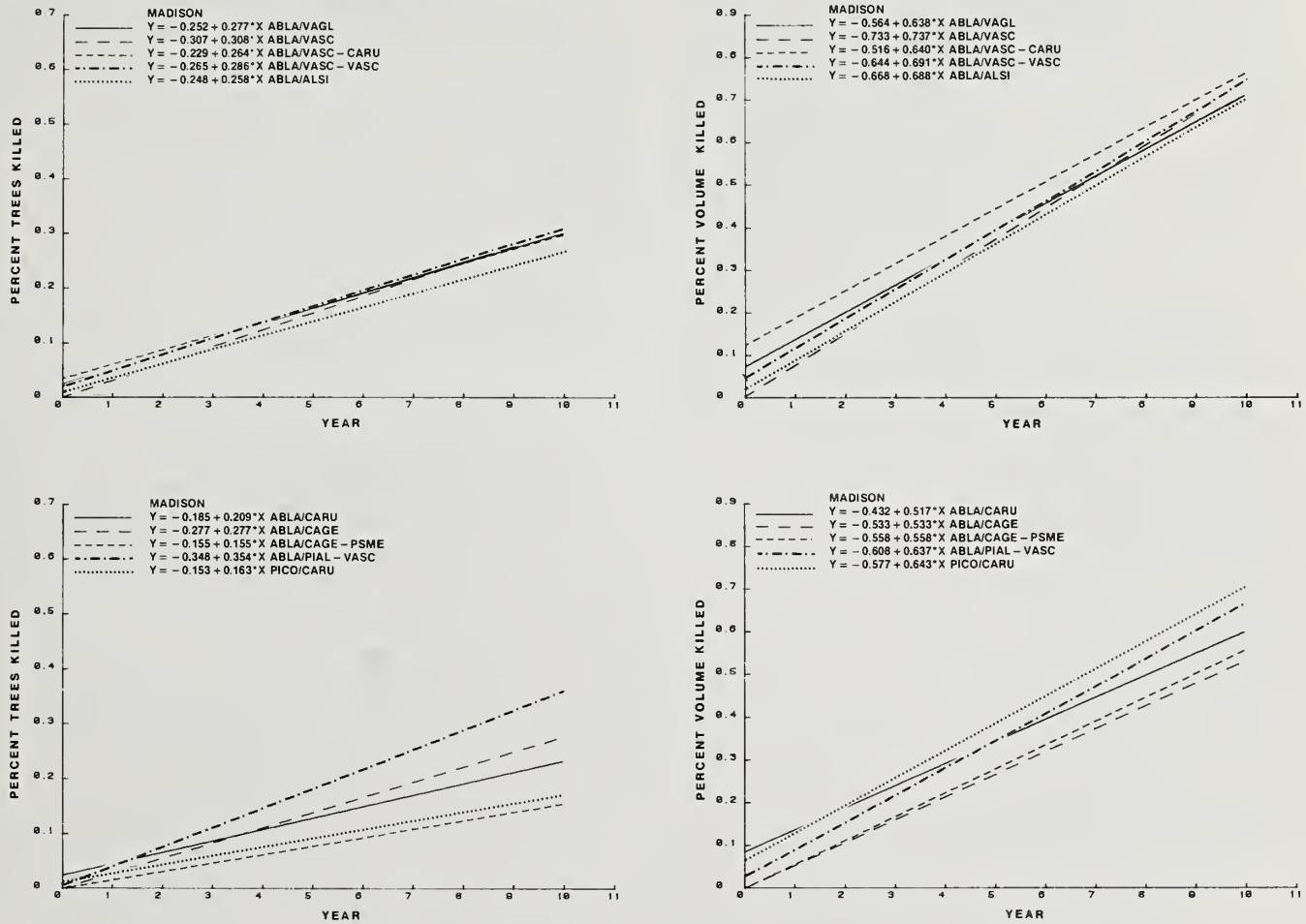
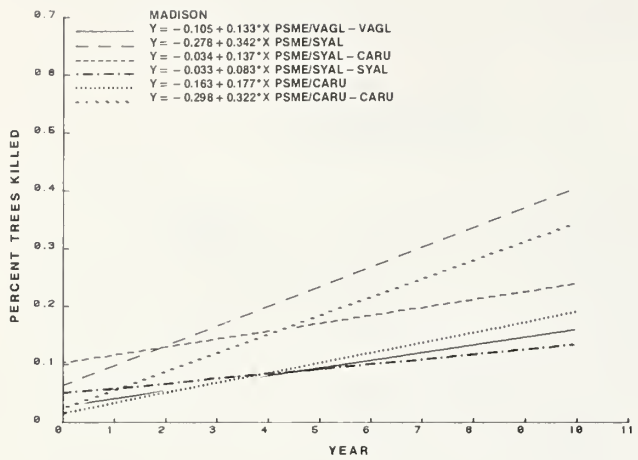
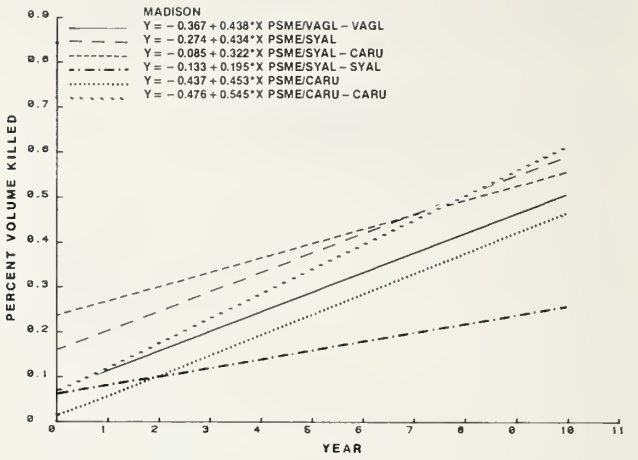
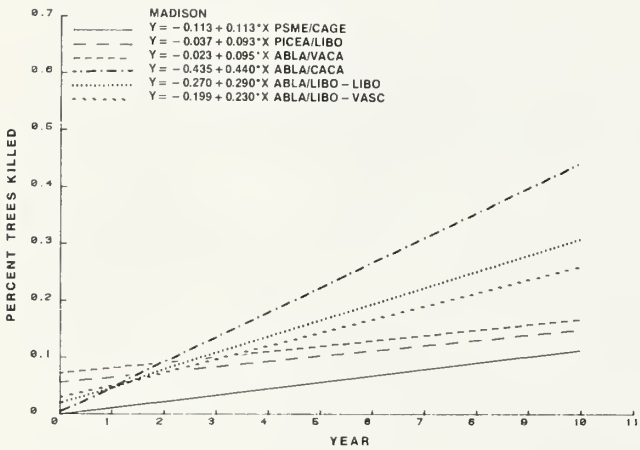
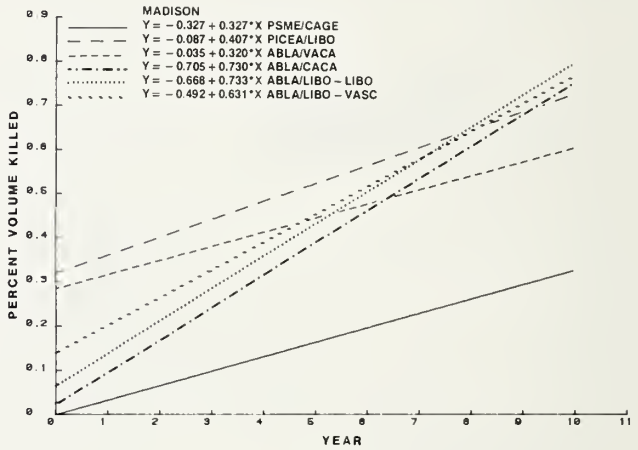


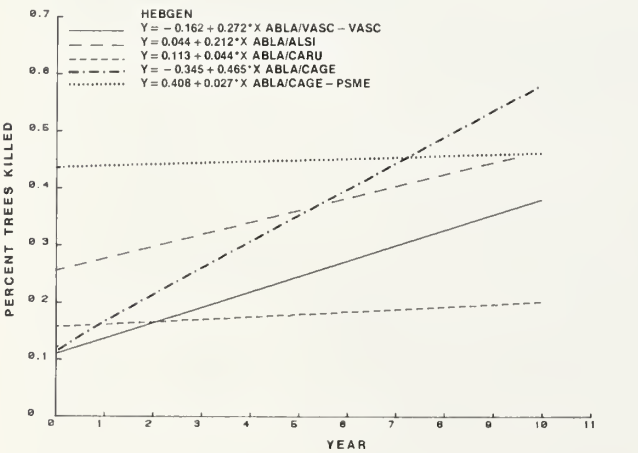
Figure 16.—Predicted numbers of lodgepole pine trees and volume losses to mountain pine beetles by habitat type over time on the Madison Ranger District, Beaverhead National Forest, and Hebgen Lake Ranger District, Gallatin National Forest, MT.

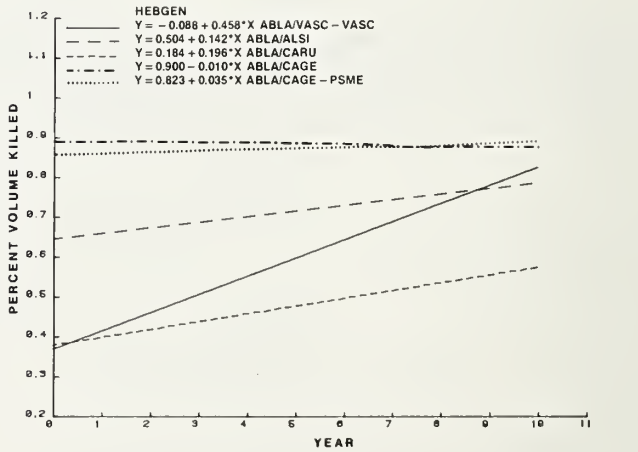

MADISON
Y = −0.105 + 0.133*X PSME/VAGL − VAGL
Y = −0.278 + 0.342*X PSME/SYAL
Y = −0.034 + 0.137*X PSME/SYAL − CARU
Y = −0.033 + 0.083*X PSME/SYAL − SYAL
Y = −0.163 + 0.177*X PSME/CARU
Y = −0.298 + 0.322*X PSME/CARU − CARU
PERCENT TREES KILLED
YEAR


MADISON
Y = −0.367 + 0.438*X PSME/VAGL − VAGL
Y = −0.274 + 0.434*X PSME/SYAL
Y = −0.085 + 0.322*X PSME/SYAL − CARU
Y = −0.133 + 0.195*X PSME/SYAL − SYAL
Y = −0.437 + 0.453*X PSME/CARU
Y = −0.476 + 0.545*X PSME/CARU − CARU
PERCENT VOLUME KILLED
YEAR


MADISON
Y = −0.113 + 0.113*X PSME/CAGE
Y = −0.037 + 0.093*X PICEA/LIBO
Y = −0.023 + 0.095*X ABLA/VACA
Y = −0.435 + 0.440*X ABLA/CACA
Y = −0.270 + 0.290*X ABLA/LIBO − LIBO
Y = −0.199 + 0.230*X ABLA/LIBO − VASC
PERCENT TREES KILLED
YEAR


MADISON
Y = −0.327 + 0.327*X PSME/CAGE
Y = −0.087 + 0.407*X PICEA/LIBO
Y = −0.035 + 0.320*X ABLA/VACA
Y = −0.705 + 0.730*X ABLA/CACA
Y = −0.668 + 0.733*X ABLA/LIBO − LIBO
Y = −0.492 + 0.631*X ABLA/LIBO − VASC
PERCENT VOLUME KILLED
YEAR


HEBGEN
Y = −0.162 + 0.272*X ABLA/VASC − VASC
Y = 0.044 + 0.212*X ABLA/ALSI
Y = 0.113 + 0.044*X ABLA/CARU
Y = −0.345 + 0.465*X ABLA/CAGE
Y = 0.408 + 0.027*X ABLA/CAGE − PSME
PERCENT TREES KILLED
YEAR


HEBGEN
Y = −0.088 + 0.458*X ABLA/VASC − VASC
Y = 0.504 + 0.142*X ABLA/ALSI
Y = 0.184 + 0.196*X ABLA/CARU
Y = 0.900 − 0.010*X ABLA/CAGE
Y = 0.823 + 0.035*X ABLA/CAGE − PSME
PERCENT VOLUME KILLED
YEAR

In some habitat types, tree mortality increases rapidly, and most susceptible trees and volume are killed in a relatively short time (fig. 17: ABLA/VASC-VASC, ABLA/ALSI). In others, mortality may occur over 10 years and never exceed 30 percent of the stand (fig. 17: ABLA/CARU, ABLA/LIBO-LIBO). All susceptible trees may be killed in other habitat types, but it may require 8 to 10 years. Thus, habitat type is an important consideration when attempting to predict tree losses.

Knowledge of tree losses to mountain pine beetles, by habitat type in conjunction with timber inventory data, can be used to prepare maps showing stands of various hazard to beetle infestation and loss. Historical maps have been used to draw attention to areas that have suffered repeated severe outbreaks of beetles (Crookston and others 1977). Yearly maps prepared for current outbreaks show rate of infestation spread and help delineate stands of various hazard.

Maps prepared from output of the INDIDS/rate of loss model can be used by managers to initiate strategies to prevent future infestations or to salvage logs and reduce fuel loads in stands where mountain pine beetle infestations have occurred. Usually, managers can expect that another epidemic will ensue within 20 to 40 years, when remaining trees reach size classes with phloem thickness conducive to population buildup (Amman 1975). However, this depends on characteristics of stands and how soon residual trees become susceptible. For example, management may be postponed until the next decade, if predicted stand mortality does not exceed 20 to 30 percent over 10 years. Meanwhile, stands can be assessed and management implemented in those stands containing habitat types and structure where considerable tree mortality or volume loss is predicted to occur over a short time. By putting the higher risk stands under management, loss would probably be prevented in some high, many moderate, and many low risk stands.

Model use.—Answers to the questions, "Which of the lodgepole pine stands are the most susceptible to mountain pine beetle outbreak development?" and "How many trees will the manager lose if a stand becomes infested?" are dependent upon risk. A definition of risk has two components: (1) probability of an outbreak within a set time and (2) expected loss in the advent of an outbreak (Safranyik 1982). Reliable methods are not available to predict when an outbreak will develop, but we can predict the most susceptible stands and stand depletion in terms of stand structure.

The Forest Service currently uses FORPLAN, a linear programming model (Johnson and others 1980), for land management planning (land use allocation and the scheduling of management activities). The management activities and associated outputs, costs, and environmental effects used in FORPLAN are presented in prescriptions for stands within analysis areas. In the Forest Service Northern Region, analysis areas are lands that meet certain common classification criteria; these lands are not usually contiguous. Classification criteria include habitat type, timber size class, slope class, or other characteristics.

Using FORPLAN, one approach to modeling tree mortality caused by mountain pine beetles has been to predict susceptible areas in analysis areas, which ones would be affected, and the resulting mortality over two decades. While it might be possible to predict rate of loss from beetles throughout the forest, this information would be of little value for adjusting yield tables if the locations of high, moderate, and low risk stands are not identified within analysis areas. The FORPLAN model would spread bark beetle effects over the next two decades for all stands within analysis areas, which would not allow scheduling earlier harvest of stands with a high probability of infestation and mortality within analysis areas.

An alternative approach is recommended when the locations of stands within analysis areas are identified through timber or stand examination surveys. Beetle attack may then be simulated by the rate of loss model, which shows the effects of an epidemic in the absence of timber management. If other management practices are not implemented, it will be necessary to constrain the predicted tree loss by assignment to a certain acreage. Thus, there would be two prescriptions—one for some stands in parts of the analysis area with infestation, and one for other parts with no effects of infestation.

As an example, stands on the Helena National Forest were analyzed in a FORPLAN run by grouping habitat types so mortality factors could be directly applied to yield tables. A procedure was adopted and used to adjust yield tables based on the coefficients developed for the Helena National Forest plan (Brohman and others 1982). Coefficients were based on the assumption that a 50 percent loss of lodgepole pine would occur over 5 years. If so, then 25 percent of the loss would occur by year 5, and the remaining 75 percent would occur by year 10. The estimated loss as a percentage of volume by age classes was determined as shown:

$$Y_{1'} = Y_1 (1 - \tfrac{1}{4} L)$$
$$Y_{2'} = Y_2 (1 - \tfrac{3}{4} L)$$
$$Y_{j'} = Y_j (1 - L),\ j > 3$$

where

L = proportion of volume lost to beetles (50 percent = 0.50),

Y_j = tabular volume for decade j of the plan, and

$Y_{j'}$ = adjusted volume expected to exist in decade j.

Such coefficients must be derived for each habitat type or habitat type group to be applicable to the model. Note that the decade 1, 2, or 3 of the Forest plan may correspond to different decades in the yield table for different stands or habitat type groups within analysis areas. For example, if groups of stands are 105 years old, then Y_1 is the tabular yield shown at 110 years (25 percent loss by year 5). If the current age is 165 years, then Y_1 is the tabular yield shown for 170 years (25 percent loss by year 5, and 75 percent loss by year 10 at 175 years). The graphs in figure 18 were developed using this approach, coupled with the INDIDS/rate of loss model for the Helena National Forest in the absence of beetle attack. The factor or proportionality is (1−L), the proportion of stand volume not killed.

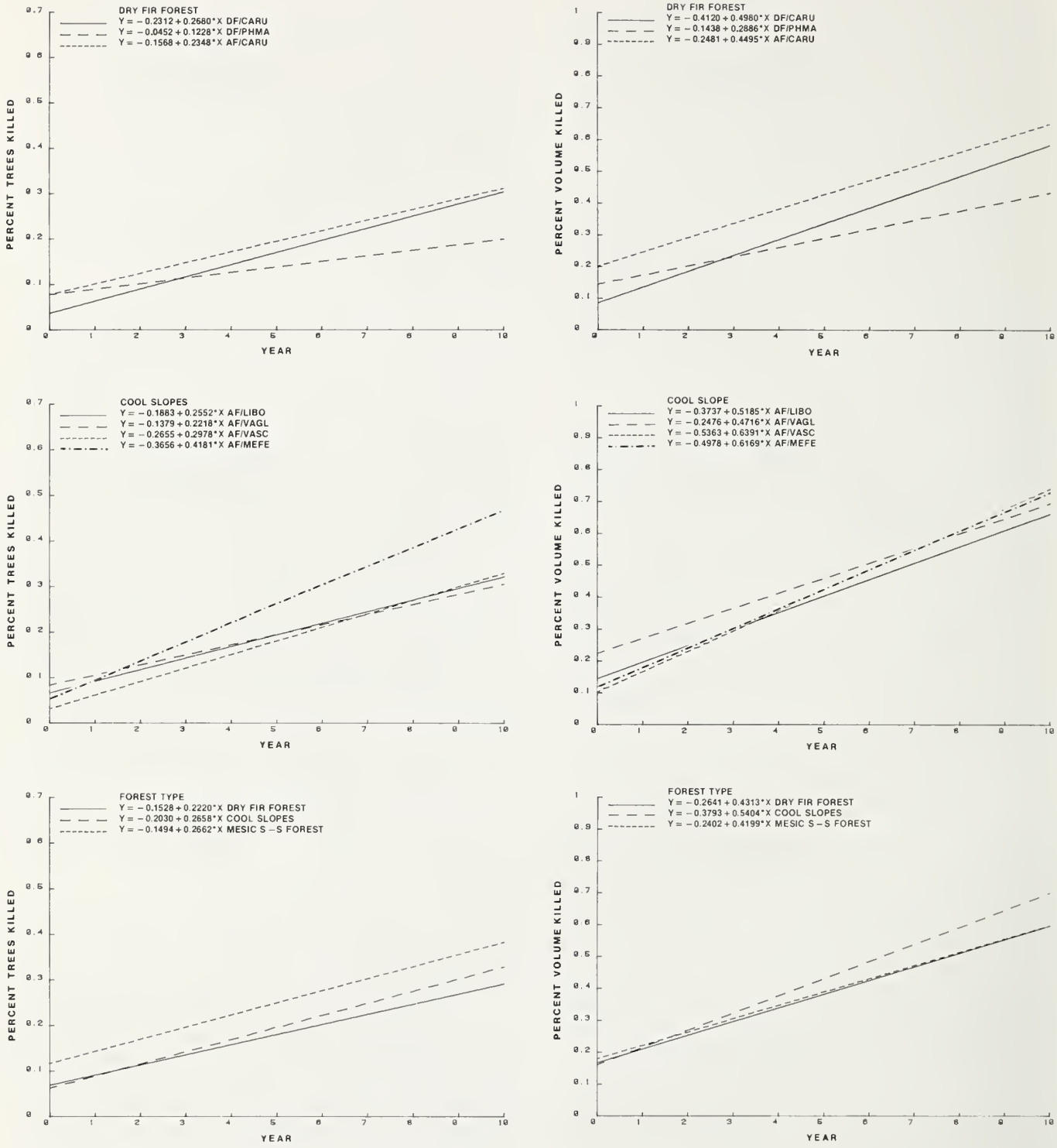


Figure 17.—Projected lodgepole pine tree and volume losses to mountain pine beetles, from the rate of loss-INDIDS model, within habitat type groups on dry cool slopes and mesic sites on Helena National Forest, MT.

The final step in the FORPLAN run for the Helena National Forest plan was to adjust existing yield tables by the appropriate coefficient for each habitat type group. Regenerated stands were not adjusted, because management should prevent mountain pine beetle outbreaks over a rotation. The assumption that the beetle will infest susceptible stands over the Forest in the next 20 years may not be totally correct, but it seems highly probable, based on available information. By including coefficients in the yield tables, the FORPLAN model should show which highly susceptible lodgepole stands need immediate harvesting, and which stands should be harvested before becoming highly susceptible. By using assessments from FORPLAN and loss predictions from the INDIDS/rate of loss model, harvesting can be accomplished in high hazard, susceptible stands before an epidemic develops, thus minimizing tree mortality caused by beetles.

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APPENDIX

The appendix contains mathematical counterparts of graphic models portrayed in figures 1, 5, 6, and 7. FORTRAN statements from Cole and others (1976) are used for brevity. In the event that highly repetitive computer use is made of the mathematical forms, as in simulation, some added computer efficiency may be achieved with further simplification.

FORTRAN Statements

ENDEMIC GREEN STAND (GS)

```
YR = 1
   GS = 26. 96*EXP(-(ABS(((DBH+18)/
        26.5-1)/.205)**1.8))+.2
LIMIT
  4 ≤ DBH ≤ 30
```

ANNUAL MORTALITY PERCENT (AM)

```
6 ≤ YR ≤ 8
    TI = .235*EXP(-(ABS(((30-DBH)/
         25.5-1)/.225)**1.8))+.365
    EL = EXP(-(ABS(((YR-5.5)/2.5-1)/
         (1-TI))**1.8))
    ER = EXP(-((1/(1-TI))**1.8))
9 ≤ YR ≤ 11
    TI = .055*EXP(-(ABS(((30-DBH)/
         25.5-1)/.35)**3))+.47
    EL = EXP(-(ABS(((11.5-YR)/3.5-1)/
         (1-TI))**1.9))
    ER = EXP(-((1/(1-TI))**1.9))
6 ≤ YR ≤ 11
    YP = .3295*EXP(-(ABS(((DBH-4)/
         26-1)/.8)**4.5))-.0215
    AM = 97.765*YP*((EL-ER)/(1-ER))
LIMITS
  4 ≤ DBH ≤ 30, 1 ≤ YR ≤ 11, integer values only
LIMITS FOR ALL BROOD MODELS
  4 ≤ DBH ≤ 30, 1 ≤ YR ≤ 13, integer values only
```

EGGS (EG)

```
FOR 1 ≤ YR ≤ 11.8
    BP = 177.918*EXP(-(ABS((DBH/35-1)/
         .85)**3))-34.918
    TI = .9533*EXP(-(ABS(((35-DBH)/
         35-1)/.63)**2.6))-.0333
     G = ABS(((YR-1)/10.8-1)/(1-TI))**1.6
     P = 1.6
FOR 11.8 < YR ≤ 13
    BP = 0
    TI = .42*EXP(-(ABS(((35-DBH)/35-1)/
         .605)**5))+.25
     G = ABS((17-YR)/5.2-1)/(1-TI))**3
     P = 3
FOR 1 ≤ YR ≤ 13
    YP = 349.251*EXP(-(ABS((DBH/35-1)/
         .68)**3.2))-11.251
    ER = EXP(-(1/(1-TI))**P)
    EG = ((EXP(-(G))-ER)/(1-ER)*
         (YP-BP)+BP)**1.0144
```

SMALL LARVAE (SL)

```
FOR 1 ≤ YR ≤ 10
    BP = 50.186*EXP(-(ABS((DBH/35-1)/
         .682)**4.5))-.186
    TI = .105*EXP(-(ABS(((35-DBH)/
         35-1)/.51)**5))+.565
     G = ABS((YR/10-1)/(1-TI))**2.6
     P = 2.6
FOR 11 ≤ YR ≤ 13
    BP = 45*EXP(-(ABS((DBH/35-1)/
         .593)**4))+1
     A = .00025396*(35-DBH)**2.1+.001
    TI = .405*EXP(-(ABS(((35-DBH)/
         35-1)/.146)**2.6))+A
     G = ABS(((13-YR)/3-1)/(1-TI))**2.4
     P = 2.4
FOR 1 ≤ YR ≤ 13
    YP = 98.53*EXP(-(ABS((DBH/35-1)/
         .716)**3.6))-3.53
    ER = EXP(-(1/(1-TI))**P)
    SL = ((EXP(-(G))-ER)/(1-ER)*
         (YP-BP)+BP)*.9565
```

LARGE LARVAE (LL)

```
FOR 1 ≤ YR ≤ 8
    BP = 31.093*EXP(-(ABS((DBH/35-1)/
         .664)**4.3))-.093
    TI = .07598*EXP(-(ABS(((DBH-4)/
         31-1)/.83)**5))+.704
FOR 9 ≤ YR ≤ 13
    BP = 15*EXP(-(ABS((DBH/35-1)/
         .625)**7))+1
    TI = .1073*EXP(-(ABS((DBH/35-1)/
         .674)**3.4))+.708
FOR 1 ≤ YR ≤ 13
    YP = 52.117*EXP(-(ABS((DBH/35-1)/
         .695)**3.7))+.883
    LL = (EXP(-(ABS((YR/8-1)/(1-TI))**
         1.5))*(YP-BP)+BP)*.9865
```

EMERGENCE (EM)

```
FOR 1 ≤ YR ≤ 7
    BP = 17*EXP(-(ABS((DBH/35-1)/
         .655)**6))
     P = 2.3*EXP(-(ABS(((35-DBH)/29-1)/
         .13)**2.2))+2.2
     G = ABS((YR/7.7-1)/.2)**P
FOR 8 ≤ YR ≤ 13
    BP = .13*DBH
    TI = .051/*EXP(-(ABS(((35-DBH)/
         29-1)/.38**7))+.69
     G = ABS((YR/7.7-1)/(1-TI))**1.6
FOR 1 ≤ YR ≤ 13
    YP = 30.328*EXP(-(ABS((DBH/35-1)/
         .715)**4.5))+2.672
    EM = (EXP(-(G))*(YP-BP)+BP)*.995
```


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Mountain pine beetle dynamics in lodgepole pine forests. Part III: Sampling and modeling of mountain pine beetle populations. General Technical Report INT-188. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1985. 46 p.

This is the last of a three-part series on the mountain pine beetle in lodgepole pine forests. Part III contains original research, a review of published literature primarily on epidemic beetle populations, and sampling and modeling of beetle populations. Sampling methods are available for within-tree populations of beetles, tree losses within stands, and tree losses over large forested areas by aerial means. Models include beetle generation survival, beetle aggregation, lodgepole pine stand-beetle interactions, and rate and amount of tree loss in stands.

KEYWORDS: Scolytidae, *Dendroctonus ponderosae, Pinus contorta*, population dynamics, sampling, modeling

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